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Plant macrofossils from the Rhaetian of Einberg near Coburg (Bavaria, Germany). Part 2. Cycadophyta and Ginkgophyta

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

With 8 figures and 2 tables

Abstract: A plant macrofossil assemblage from Rhaetian strata of a quarry near Einberg (Franconia, Germany) comprises a diverse array of cycadophyte and ginkgophyte remains. These are described by means of macromorphology and epidermal anatomy. Three cycadalean and two bennettitalean species have been identified (*Pseudoctenis cteniforme*, *Nilssonia* sp. and *Becklesia* sp.; *Pterophyllum aequale* and *Pterophyllum zygotacticum*). Moreover, some unidentifiable cycadophyte leaf fragments have been encountered. Ginkgoales and Czekanowskiales are represented by *Sphenobaiera boegildiana* and putatively *Arberophyllum* sp., and by *Czekanowskia nathorstii* and *Leptostrobus* sp., respectively. A comparison between the flora from Einberg with the Rhaetian floras of adjacent localities (viz. Wüstenwelsberg, Heilgersdorf and Kipfendorf) reveals distinct regional differences in the cycadalean, bennettitalean and ginkgoalean portions 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.

Key words: Late Triassic, Franconia, Cycadales, Bennettitales, Ginkgoales, Czekanowskiales.

1. Introduction

Triassic–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 KONIJNENBURG-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 KONIJNENBURG-VAN CITTERT et al. 2014; VAN KONIJNENBURG-VAN CITTERT et al. 2016; VAN KONIJNENBURG-VAN CITTERT

et al. 2017; VAN KONIJNENBURG-VAN CITTERT et al. 2018; VAN KONIJNENBURG-VAN CITTERT et al. 2019; VAN KONIJNENBURG-VAN CITTERT et al. 2020; VAN KONIJNENBURG-VAN CITTERT et al. 2021a; POTT et al. 2016); this flora may be the best-known Rhaetian flora from the area right now.

The slightly less diverse flora from the Rhaetian sandstone of Einberg, also near Coburg, is now the subject for study. As the flora turned out to be more diverse than it was originally thought to be, the flora is described in three parts. The remains of ferns, fern allies and seed ferns have been published recently (VAN KONIJNENBURG-VAN CITTERT et al. 2021b). The present study deals with further gymnosperm groups except for the conifers that will be the subject of the third publication.

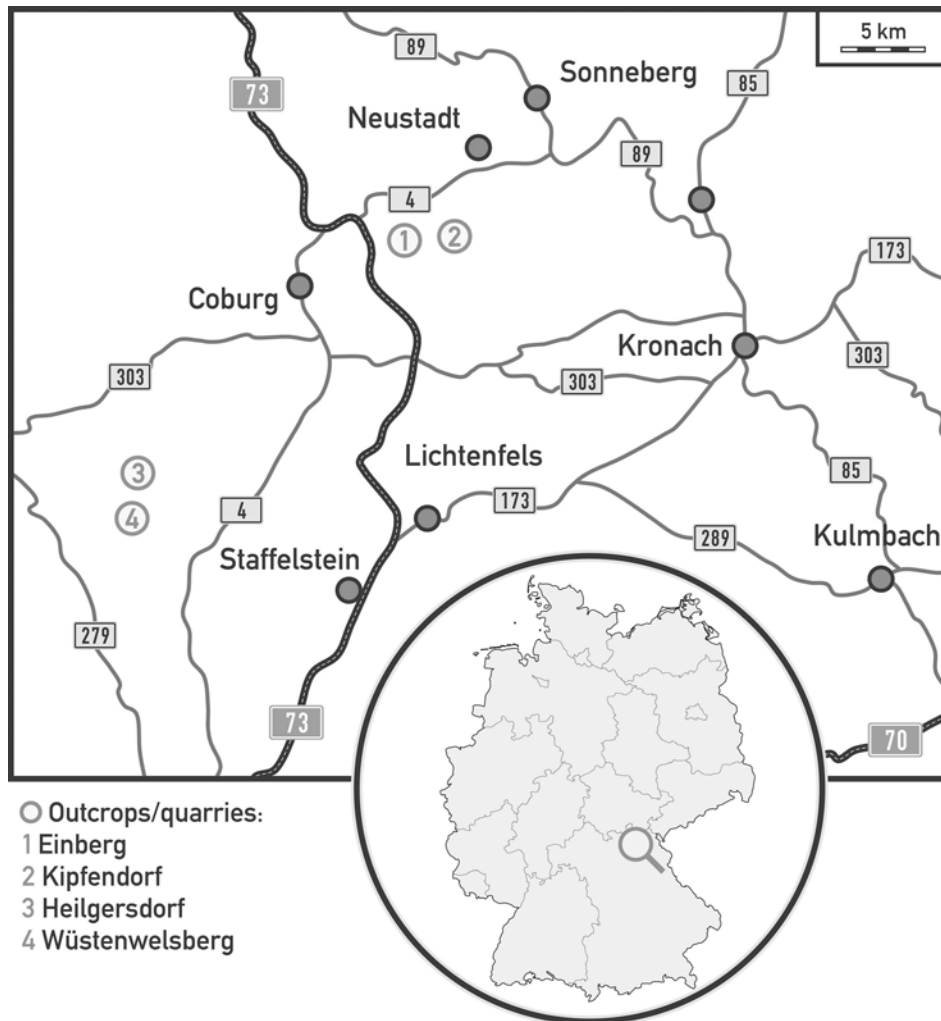


Fig. 1. Map of Germany indicating the position of the locality Einberg near Coburg in Franconia (Bavaria), and the position of the other three Rhaetian localities in the same area: Wüstenwelsberg, Heilgersdorf and Kipfendorf.

Additional small quarries around Coburg with Rhaetian–Hettangian strata yielding plant macrofossils are located near Heilgersdorf (KELBER & VAN KONIJNENBURG-VAN CITTERT 1997) and Kipfendorf (Fig. 1). Kipfendorf represents a historical locality not accessible anymore (FISCHER 1907; KRUMBECK 1939; ACHILLES 1981; for details see VAN KONIJNENBURG-VAN CITTERT et al. 2021b). From Heilgersdorf, 15 taxa have been reported from the plant macrofossil assemblage (KELBER & VAN KONIJNENBURG-VAN CITTERT 1997), whereas the Wüstenwelsberg flora is much more diverse comprising at least 40 taxa. It can, however, not be excluded that the higher diversity recorded from the latter out-

crop 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 the analysis of cuticles. Based on the latter, the composition of the Rhaetian flora from the area had been revised slightly, shaping an image of an articulated landscape covered by a complex, multi-storeyed vegetation (VAN KONIJNENBURG-VAN CITTERT et al. 2021a; VAN KONIJNENBURG-VAN CITTERT et al. 2021b). Hygrophytic elements such as lycophytes, sphenophytes and ferns are well represented in the various localities. Gymnosperms probably adapted to moister environments such as some bennettitaleans, cycads and ginkgophytes are abundant and diverse. Even the

most xerophytic among the gymnosperms, seed ferns and conifers show epidermal anatomies reminiscent of adaptations to increased humidity coupled with appropriate environmental conditions.

The present study deals with the relatively rare cycadophytes and ginkgophytes, a third paper will deal with the numerous conifer remains from the Einberg Quarry.

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 Rödental, 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 (NITSCH *et al.* 2011) is exposed. 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 VAN KONIJENBURG-VAN CITTERT *et al.* (2021b).

Although a detailed lithological profile of the outcrop at Einberg was never recorded, 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 supports an assignment of the fossiliferous strata to the Triletes beds of 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. 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 % HNO₃ with a few crystals of KClO₃) and subsequently treated with 5–10 % ammonia (NH₄OH) 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 paraplax. The slides are stored in the collection of the Laboratory of Palaeobotany and Palynology, Utrecht University, 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 lighting 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 on-screen by using a high-resolution imaging software.

3. Systematic palaeobotany

Order Cycadales PERSOON ex BERCHTOLD *et*
PRESL 1820
Incertae familiae
Genus *Pseudoctenis* SEWARD 1911

Pseudoctenis cteniforme (NATHORST) HARRIS 1950
Figs. 2A, 4A, B

Selected synonymy:

- 1878 *Pterophyllum?* *cteniforme* NATHORST, p. 47, pl. 14, fig. 1.
1933 *Pseudopterophyllum cteniforme* (NATHORST). – FLORIN, p. 81, pl. 9, figs. 1–7, text-figs. 28, 29.
1950 *Pseudoctenis cteniforme* (NATHORST). – HARRIS, p. 1018, no illustration.

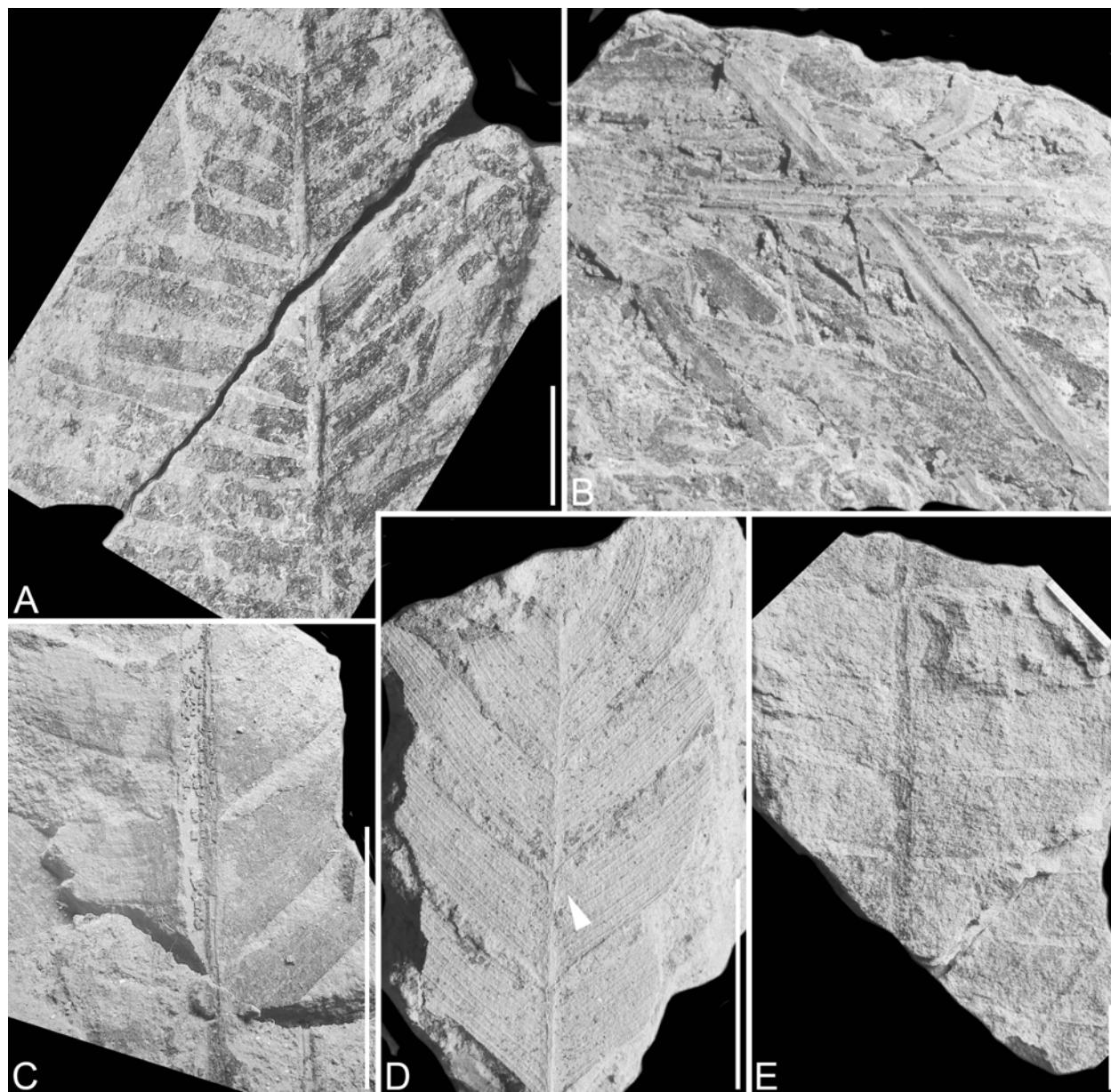


Fig. 2. *Pseudoctenis cteniforme*, *Becklesia* sp., *Nilssonina* sp. and *Pterophyllum aequale* from the Rhaetian of Einberg. **A** – *Pseudoctenis cteniforme*, pinnate leaf fragment; O527/02. **B** – *Becklesia* sp., several detached leaves; 14Ei00. **C** – *Nilssonina* sp., leaf fragment with clear venation; O507/01. **D** – *Nilssonina* sp., leaf fragment with five oppositely inserted pairs of pinnae, arrow indicates vein bifurcation; O583/00. **E** – *Pterophyllum aequale*, frond fragment; O169/98. Scale bars equal 10 mm.

2018 *Pseudoctenis cteniforme* (NATHORST) HARRIS. – VAN KONIJNENBURG-VAN CITTERT et al., *cum syn.*, p. 206, pl. 9, figs. 1–4, pl. 10, figs. 5–6.

Material studied: O125/98+126/98+127/98, 140/98, 422/01, 426/01+427/01, 527/02.

Description: There is one good specimen of *Pseudoctenis cteniforme* in the Einberg collection and a couple of less well-preserved ones. Specimen O527/02 (Fig. 2A) is a pinnate leaf fragment 60.6 mm long and max. 43 mm wide. It is seen from below with a 1.5 mm wide rachis that bears 15 pairs of (sub)oppositely

inserted pinnae, at c. 60°–70°. Pinnae usually touch but never overlap; sometimes there is a small gap in between them. None of the pinnae is complete; the longest pinna fragment is 28.6 mm long and all pinnae fragments are between 3 mm (for the more distal ones) and 2 mm (for the more apical ones) wide. The veins run parallel to the margin at a concentration of c. 12–15 veins/cm (commonly there are 3 to 6 veins in a pinna) (Fig. 2A). Specimens O125+126+127/98, O140/98 and 426/01+427/01 all yield typical but smaller pinnate leaf fragments, which either provided no cuticle at all or small, poorly preserved cuticle fragments only.

From O527/02, relatively good cuticular remains could be obtained. The leaf is hypostomatic. Normal epidermal cells are isodiametric to slightly elongate, and irregular in shape. Veins are indicated by more elongate epidermal cells (Fig. 4A). The lower cuticle shows slightly sunken stomata, sometimes arranged in short rows, sometimes more evenly distributed between the veins (Fig. 4B). The lateral of the 4–6 subsidiary cells are normally thickened whereas the remainder are slightly less cutinized, commonly bearing a short papilla, overhanging the stomatal pit, and reducing it to a small circular pore.

Remarks: The present species was first briefly described and figured as *Pterophyllum? cteniforme* by NATHORST (1878) from the Rhaetian of Bjuv (Scania, Sweden). FLORIN (1933) recognised the non-bennettitalean nature of the specimen and refigured the holotype by transferring it to his new genus *Pseudopterophyllum* FLORIN 1933. HARRIS (1950) transferred the species to *Pseudoctenis* SEWARD 1911, which has nomenclatorial priority over *Pseudopterophyllum*.

Before the description of the cycads from the Rhaetian of Wüstenwelsberg (VAN KONIJENBURG-VAN CITTERT et al. 2018), only the holotype of *Pseudoctenis cteniforme* (NATHORST) HARRIS 1950 was known. From Wüstenwelsberg, about 20 frond and pinna fragments have been described (VAN KONIJENBURG-VAN CITTERT et al. 2018), and here we record its presence in Einberg, albeit with less material. Specimen O527/02 is the largest specimen and is very similar to the one figured in VAN KONIJENBURG-VAN CITTERT et al. (2018, pl. 9, fig. 1), both in macromorphology and cuticular details. The other specimens are smaller pinnate leaf fragments but agree as well in macromorphology. KELBER & VAN KONIJENBURG-VAN CITTERT (1997) mentioned a specimen from Heilgersdorf as *Pseudoctenis* sp., but it was an unfigured,

small leaf fragment only, not suitable for a close comparison. For a more elaborate discussion, we refer to VAN KONIJENBURG-VAN CITTERT et al. (2018).

Occurrences in other adjacent Rhaetian floras: Sweden: NATHORST (1878), FLORIN (1933).

Incertae familiae

Genus *Becklesia* SEWARD 1895

Becklesia sp.

Figs. 2B, 4C, D

Material studied: O77/98, 89/98, 290/00, 326/00; 14Ei00, 28Ei01, 28Ei01. Cuticle slides without a remaining specimen: C. 340, 345, 346 ‘Leaf with clear midrib’.

Description: There are a few leaf remains that resemble *Becklesia franconica* in macromorphology (VAN KONIJENBURG-VAN CITTERT 2021a, pl. 4 figs 3, 5). 14Ei00 shows a couple of leaves with distinct central depressions just as in *Becklesia franconica*. The longest leaf fragment is 36 mm long and increases in width from 1.7 to 3.1 mm (Fig. 2B). O77/98 is a similar fragment, 52 mm long and up to 3.9 mm wide, again with a deep central depression. The other specimens display smaller leaf fragments. 14Ei00 yielded some poorly preserved cuticle fragments (Figs. 4D) just as O290/00 and there are also a few cuticle slides without remaining macro specimen (C. 340, 345, 34; Fig. 4C). These cuticle remains differ from those of *Becklesia franconica* from Wüstenwelsberg in having papillate subsidiary cells, and normal epidermal cells also may carry small papillae (Fig. 4D). The arrangement of the two stomatal bands, each on a side of a large stomatal free zone with elongate epidermal cells (indicating the central depression) is the same as in *Becklesia franconica* (Fig. 4C).

Remarks: Macromorphologically, the *Becklesia* remains from Einberg are identical with those from Wüstenwelsberg, but the presence of the papillae on the subsidiary cells and normal epidermal cells brings us to describe them only as *Becklesia* sp. It is possible that we are still dealing with the same species, and that the presence of these papillae can be explained by environmental influences, but for an undisputable identification, more and better preserved material is needed.

Order Nilssoniales THOMAS et BANCROFT 1913
 Family Nilssonaceae KIMURA et SEDIKO 1975
 Genus *Nilssonia* BRONGNIART 1825

Nilssonia sp.
 Figs. 2C, D, 4E

Material studied: O287/00+288/00+583/00, 506+507/01.

Description: Only two small fragments of *Nilssonia* leaves have been encountered in the Einberg assemblage. The first consists of O287/00+288/00 that belong together, with O583/00 as the apical part of its counterpart. The leaf fragment (Fig. 2D) has a 1-mm-wide rachis with remains of five opposite pairs of pinnae with a concave adaxial margin and a convex abaxial margin. Pinnae touch but never overlap. The uppermost two pinna pairs are curving forward. None of the pinnae is complete but the uppermost one in O583/00 is almost complete and 12.0 mm long and 2.3 mm wide. The second fragment, O506/01 and 507/01 (Fig. 2C) are part and counterpart, is again an apical but even smaller fragment. Here, the pinnae are suboppositely attached to the rachis and for the rest agree with the other specimen; venation in both specimens is parallel with fine veins that only very rarely bifurcate once near the pinna base (Fig. 2D, arrow). We could obtain some cuticle fragments from O506/01 (Fig. 4E). The cuticle is thin and brittle with polygonal, irregular epidermal cells, sometimes with slightly sinuous cell walls. Veins are indicated by slightly more elongate cells. The lower cuticle is characterised by irregularly placed stomata with slightly sunken guard cells, surrounded by 3–5 even subsidiary cells (Fig. 4E, inset).

Remarks: These two small leaf fragments can be assigned to *Nilssonia* based on their macromorphology with the pinnae almost completely covering the rachis on the upper side and the parallel venation of the pinnae commonly without showing signs of a bifurcation (Fig. 2D).

The cuticle fragments recovered from O506/01 are very characteristic of *Nilssonia* as well. However, both the specimens and the cuticle fragments are too fragmentarily preserved to being confidently assigned to a distinct species. Only one *Nilssonia* species (viz. *Nilssonia pterophylloides* NATHORST 1879) was found in the Wüstenwelsberg assemblage, but

this taxon is completely different from the Einberg material in its differently shaped and much larger pinnae (VAN KONIJENBURG-VAN CITTERT et al. 2018). Comparable material has not been found at Heilgersdorf (KELBER & VAN KONIJENBURG-VAN CITTERT 1997) nor Kipfendorf, although ACHILLES (1981) mentioned the presence of *Nilssonia minima* GOTHAN in the list of macrofossils from the locality; some larger specimens of that species can be macromorphologically similar to our *Nilssonia* sp. In addition, FISCHER (1907) mentioned the presence of *Nilssonia* from Kipfendorf, but those remains were never described nor figured, and consequently the identification of those remains cannot be verified. KELBER & VAN KONIJENBURG-VAN CITTERT (1997) described *Nilssonia polymorpha* from Heilgersdorf, but that determination is doubtful. The fossils probably belonged to an *Anomozamites* or *Pterophyllum* species, possibly *Pterophyllum aequale*.

Nilssonia minima was described by GOTHAN (1914) from a Hettangian locality near Nuremberg and has commonly much smaller pinnae than the *Nilssonia* specimens under consideration here, whose cuticle is relatively thick for a *Nilssonia*. WEBER (1968) described leaf fragments from Unternschreez near Bayreuth that commonly have narrow leaves with small pinnae but occasionally larger leaves with pinnae more or less of the same size as the Einberg specimens; as WEBER's material was only preserved as impressions, no comparison on an epidermal basis can be made. GOTHAN (1914, pl. 29, fig. 5) also described and figured a specimen from another Hettangian locality (Speikerner Tongrube) near Nuremberg as *Nilssonia* sp. that also shows some similarity to the Einberg specimens. It has the pinnae inserted to the upper side of the rachis but leaving the central portion of the rachis uncovered, which is less common in *Nilssonia*.

The macromorphologically most similar species of adjacent Rhaetian assemblages is *Nilssonia inciserrata* HARRIS 1932a from the Hettangian of Jameson Land (East Greenland), but that species differs characteristically in its cuticle with numerous hair bases and stomata with rather thickened subsidiary cells. *Nilssonia brevis* BRONGNIART 1825 from the Rhaetian of Sweden is also macromorphologically similar but has a thicker cuticle with heavily cutinised subsidiary cells (NATHORST 1909; ANTEVS 1919; HARRIS 1932a).

Order Bennettitales ENGLER 1892
 Family Williamsoniaceae CARRUTHERS 1870
 Genus *Pterophyllum* BRONGNIART 1825

Pterophyllum aequale (BRONGNIART) NATHORST 1878
 Figs. 2E, 3A, C

Selected synonymy:

- 1825 *Nilssonia? aequalis* BRONGNIART, p. 219, pl. 12, fig. 6.
 1878 *Pterophyllum aequale* BRONGNIART. – NATHORST, p. 18–19, pl. 2, fig. 13, p. 48–49; pl. 6, figs. 8–11.
 1950 *Pterophyllum compressum* LUNDBLAD, p. 56, pl. 9, figs. 9–13, pl. 10, figs. 1–6, text-figs. 20–22.
 2009 *Pterophyllum aequale* (BRONGNIART) NATHORST 1878. – POTT & MCLOUGHLIN, *cum syn.*, p. 125, pl. 2, figs. 1–12, pl. 3, figs. 1–8, text-fig. 4.
 2011 *Pterophyllum aequale* (BRONGNIART) NATHORST 1878. – POTT & MCLOUGHLIN, p. 1038, figs. 8A–D, 9C.
 2016 *Pterophyllum aequale* (BRONGNIART) NATHORST. – POTT et al., *cum syn.*, p. 99, pl. 1, figs. 1, 2, pl. 5, figs. 1, 2.

Material studied: 169/98, 252/99 +253/99, 404/00.

Description: Three small pinnate fragments of this characteristic species have been encountered in Einberg. O169/98 (Fig. 2E) is a 45.5 mm long and up to 46.0 mm wide pinnate fragment with the remains of six pinnae attached oppositely and perpendicularly to the rachis. No pinna is complete, the longest fragment is 24.0 mm long; the pinna width varies between 8.0 and 10.0 mm. O404/01 (Fig. 3C) is even smaller: a rachis with the remnants of three pairs of pinnae, suboppositely and perpendicularly attached. One pinna is complete and measures 9.0 × 6.5 mm with the rounded apex, typical for the species. This specimen yielded small pieces of cuticle, but those were too poorly preserved to describe. O252/99 (Fig. 3A) is an apical specimen in which the proximal three pairs of pinnae are attached perpendicularly and the apical three pinna pairs are attached under a smaller angle, decreasing from 70° to 45°. The longest pinna is 25.0 mm long, the pinna width decreases from proximally 5.0 mm to 3.5 mm apically.

Remarks: POTT et al. (2016) described and discussed the species in detail from the Rhaetian of Wüstenwelsberg, where *Pterophyllum aequale* is a common species, occurring massively in some layers. We refer to that discussion. The species has not with certainty been encountered at Heilgersdorf, although the

specimen figured in KELBER & VAN KONIJNENBURG-VAN CITTERT (1997, pl. 2, fig. 6) might have belonged to *Pterophyllum aequale* or to an *Anomozamites* sp. FISCHER (1907) recorded *Pterophyllum* sp. from Kipfendorf, and ACHILLES (1981) mentioned *Pterophyllum angustum* BRAUN 1843, but as the material is not available anymore in the Natural History Museum of Coburg, these determinations cannot be verified.

Occurrences in other adjacent Rhaetian floras:

Sweden: NATHORST (1878), LUNDBLAD 1950, POTT & MCLOUGHLIN (2009, 2011), Jameson Land (East Greenland): HARRIS (1932b, 1937), Donets Basin (Ukraine): STANISLAVSKI (1971), Iran: SCHWEITZER & KIRCHNER (2003).

Pterophyllum zygotacticum HARRIS 1932b
 Figs. 3B, D–F, 4F, G

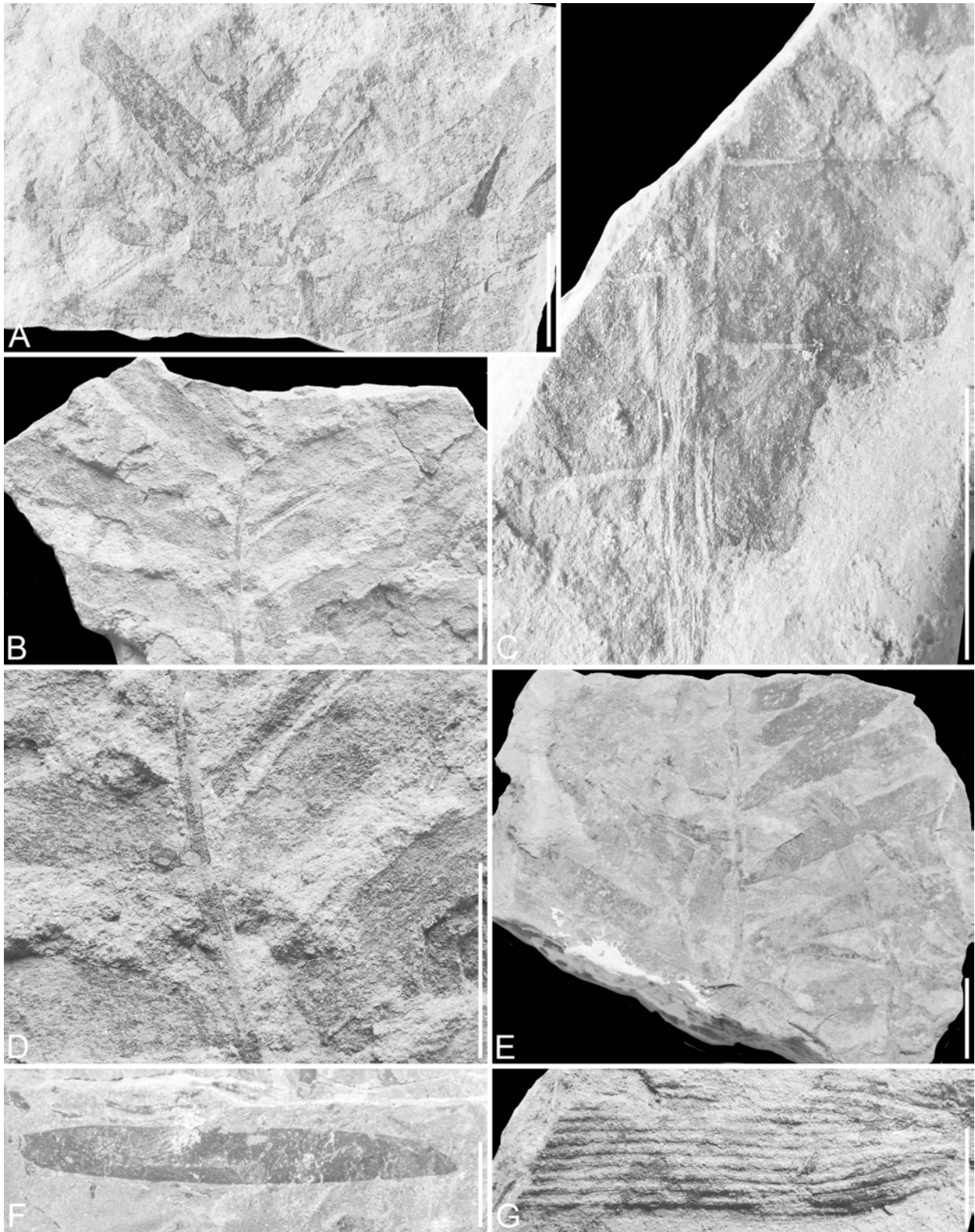
Synonymy:

- 1926 ?*Podozamites* sp. B. – HARRIS, p. 117, text-fig. 29E, F.
 1932b *Pterophyllum zygotacticum* HARRIS, p. 64, pl. 5, figs. 7, 9, 10, text-figs. 32–34.
 1937 *Pterophyllum zygotacticum* HARRIS. – HARRIS, p. 52.

Material studied: O152/98; UU25969, 25993F, 25994M, 26006.

Description: Specimen UU25993F (Fig. 3E) is the largest fragment (57.4 mm wide and 40.7 mm long). It consists of a 1-mm-wide rachis with the remains of five pairs of pinnae that are oppositely attached at an angle of c. 70° and a distance between the pairs of c. 9.0 mm. The base of the pinnae is contracted, no apices have been preserved. The longest pinna fragment is 29.6 mm long, and all pinna fragments are around 4.0 mm wide. They show a parallel venation with some bifurcations near the pinna base. O152/98 (Fig. 3B) is another leaf fragment (62.5 mm wide, 40.0 mm long) with a rachis bearing the remains of three pairs of pinnae (longest fragment 31.6 mm, 5.0 mm wide), arising at c. 60°. The parallel venation, with basal bifurcations is rather distinct (Fig. 3D). UU25969 (Fig. 3F) displays one almost complete pinna (53.0 mm long, 6.0 mm wide) with a contracted base, but the apex is missing. The venation is rather obscured by the rock matrix. The other two specimens are small pinna fragments.

UU25969 and UU25993F yielded pieces of cuticle reflecting a hypostomatic leaf. The epidermal cells of the upper cuticle are rectangular to elongate with



straight walls and without papillae. The lower cuticle is divided into narrow zones over the veins with elongate cells with somewhat sinuous cell walls, and intercostal fields with scattered stomata and hair bases. Stomata are commonly orientated transversely but sometimes in various directions, even longitudinally (Figs. 4F, G). Normal epidermal cells are isodiametric with slightly sinuous to predominantly straight cell walls, and occasionally bearing a short median papilla. The subsidiary cells are not thickened but commonly bear a papilla (Fig. 4G). Hair bases are scattered over the intercostal fields.

Remarks: HARRIS (1926) described and figured a specimen from the Rhaetian of Jameson Land as *?Podozamites* sp. B. He was not sure, whether the specimen was correctly identified as *Podozamites* or not, which was the same dilemma as we had with the Einberg material (e.g., UU25969 rather resembles a *Podozamites* leaflet), but the cuticle is characteristic of a bennettitalean leaf, just as it is in our material. HARRIS (1932b) described the specimen and new material from the same bed as *Pterophyllum zygotacticum*, including *Pterophyllum kochii* HARRIS 1926 in part (cuticle fragments, his text-fig. 17J). *Pterophyllum zygotacticum* is distinguished from other *Pterophyllum* species by, e.g., the relatively large distance between adjacent pinnae and the uniform pinna width throughout the entire leaf. Only the uppermost pinnae are slightly narrower. The cuticle is also different, especially in displaying hairs in the interveinal zones, a feature that is not very common in bennettitalean cuticles. The description of the cuticles from the Einberg specimens differs from that of HARRIS (1932b) in having somewhat sinuous epidermal cell walls (commonly straight in the Jameson Land material). Since the sample size from both localities is very small, slightly wavy epidermal cell walls might be present also in the Jameson Land material, if a larger sample would be tested. Outside Jameson Land, this species has not been recorded so far.

Occurrences in other adjacent Rhaetian floras: Jameson Land (East Greenland): HARRIS (1926, 1932b, 1937).

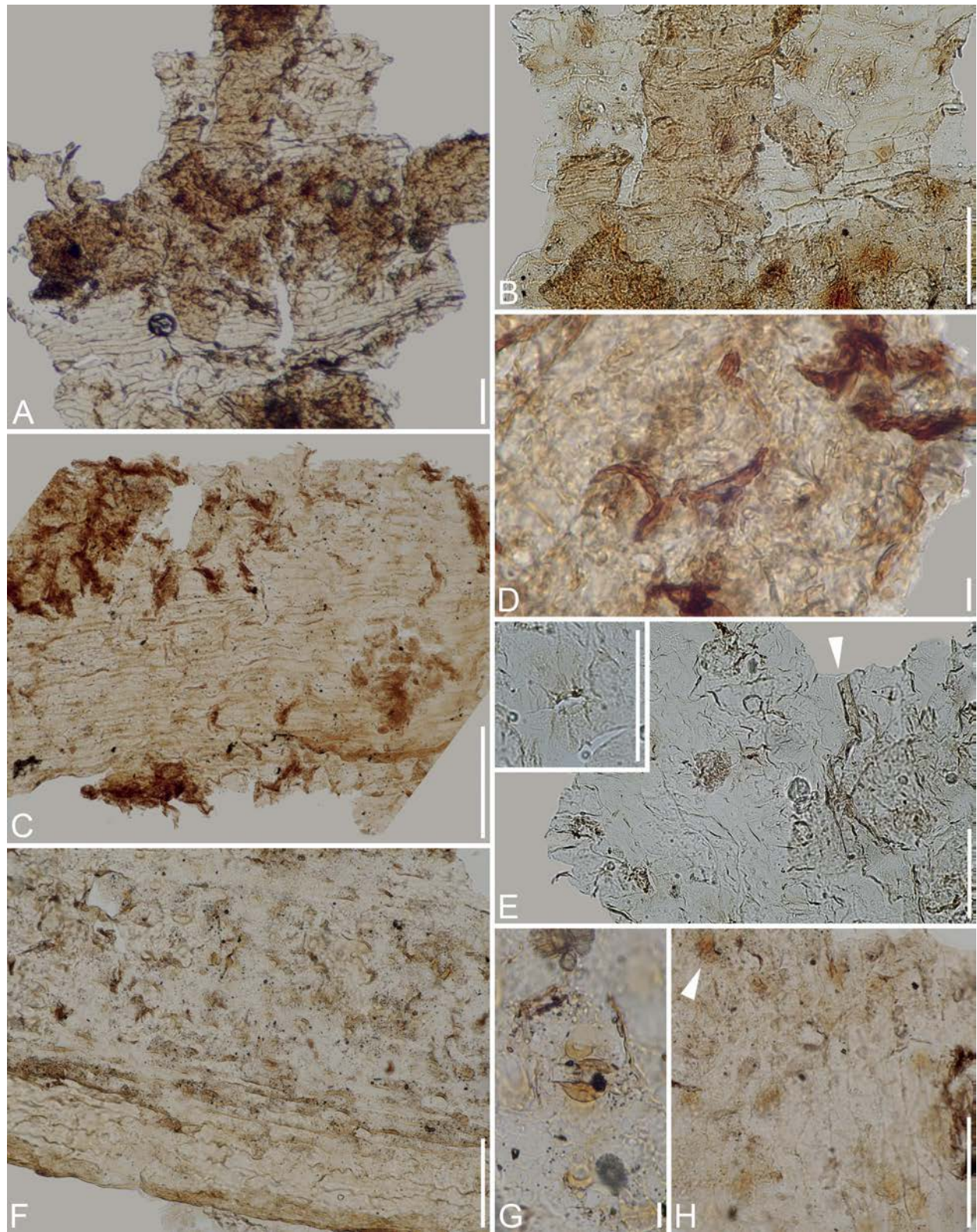
Cycadophyte leaflets
Figs. 3G, 4H

Material studied: O421/01+422/01, 434/01.

Description: Two specimens of cycadophyte leaf remains have been encountered that are too fragmentary for being assigned to any taxon, although one yielded small cuticle remains. O421/01 and its counterpart O422/01 is a fragment 24.0 mm long and 5.5 mm wide (Fig. 3G). Parallel veins can be seen at a concentration of c. 18 veins/cm. Small cuticle fragments could be prepared from O422/01 (Fig. 4H) that show irregular epidermal cells with slightly sinuous cell walls between veins that are indicated by elongate cells. Hair bases (Fig. 4H, arrow) can be observed but no stomata were found. O434/01 is a mass of leaf fragments with the same venation as O421/01+422/01 but does not provide additional information.

Remarks: Although we have some cuticle remains, the material is too fragmentary and displays too few details to make even a generic contribution. The most similar genus seems to be *Doratophyllum* HARRIS 1932a, comparable in its venation and some cuticle characters like the irregular epidermal cells and hair bases, but as no stomata were found, we cannot be sure of the attribution. *Doratophyllum nathorstii* was described from Wüstenwelsberg (VAN KONIJNENBURG-VAN CITTERT et al. 2018), but as we do not have any stomata, these fragments could theoretically even belong to *Nilssoniopteris jourdyi* (ZEILLER) FLORIN 1933. On the other hand, the vein concentration in the latter species is much higher (up to 50 veins/cm).

Fig. 3. *Pterophyllum aequale*, *Pterophyllum zygotacticum* and cycadophyte leaflet from the Rhaetian of Einberg. **A** – *Pterophyllum aequale*, apical frond fragment; O252/99. **B** – *Pterophyllum zygotacticum*, frond fragment; O152/98. **C** – *Pterophyllum aequale*, small frond fragment with typical pinnae; O404/01. **D** – *Pterophyllum zygotacticum*, detail of Fig. 3B showing venation; O152/98. **E** – *Pterophyllum zygotacticum*, largest frond fragment; UU25993F. **F** – *Pterophyllum zygotacticum*, detached pinna that yielded cuticle fragments; UU25969. **G** – Cycadophyte leaflet; O422/01. Scale bars equal 10 mm (A–F), 5 mm (G).



Order Ginkgoales GOROZHANKIN 1904
 Incertae familiae
 Genus *Sphenobaiera* FLORIN 1936

Sphenobaiera boeggildiana (HARRIS) HARRIS 1937
 Figs. 5A, 6A–C

Synonymy:

- 1935 *Baiera boeggildiana* HARRIS, p. 28, pl. 3, figs. 3, 4, pl. 4, figs. 2, 6, 8, text-fig. 14.
 1937 *Sphenobaiera boeggildiana* (HARRIS). – HARRIS, p. 58, no illustration.
 1959 *Sphenobaiera boeggildiana* (HARRIS) FLORIN. – LUNDBLAD, p. 29 (cuticle description only).

Material studied: 88Ei01.

Description: Specimen 88Ei01 is the only *Sphenobaiera* in the assemblage collected from Einberg (Fig. 5A). It consists of a leaf fragment (55.0 mm long and up to 20.0 mm wide) that is distally dissected into two lobes. The leaf fragment has a basal width of 2.0 mm that gradually increases to 12.0 mm just below the dichotomy. The two lobes are 8.5 mm and 10.0 mm wide, respectively. The leaf has a robust substance that obscures any visible venation. The cuticle is fairly thick, reflecting an almost hypostomatic leaf, but a few stomata are present on the upper cuticle. The upper cuticle (Fig. 6A) comprises isodiametric epidermal cells with wavy anticlinal walls and a commonly faint thickening of the periclinal wall. Cells over veins are of the same nature and differ from those of the intercostal fields; some indication is through slight elongation of the cells. Stomata are rare, with 4–6 subsidiary cells that are commonly papillate. The lower cuticle (Fig. 6B) shows slightly elongate cells over the veins; the epidermal cells of the intercostal fields are isodiametric, with slightly wavy anticlinal walls, and papillate. Stomata occur in the intercostal fields, are commonly longitudinally orientated, with occasional oblique or perpendicular orientation. Stomata display

4–6 subsidiary cells that commonly are papillate and obscure the sunken guard cells (Fig. 6B, C).

Remarks: HARRIS (1935) described *Baiera boeggildiana* from the Rhaetian of Jameson Land based on a few but characteristic leaves. When FLORIN (1936: 106) erected the genus *Sphenobaiera*, he discussed in which genus (*Ginkgoites* or *Sphenobaiera*) *Baiera boeggildiana* should be placed but did not make the final assignment. HARRIS (1937: 58) placed it in *Sphenobaiera*, apparently after some personal discussion with FLORIN. LUNDBLAD (1959) agreed with this assignment but attributed the combination erroneously to FLORIN.

Baiera boeggildiana differs from most Rhaetian–Hettangian *Sphenobaiera* species in being almost hypostomatic and in having isodiametric epidermal cells with wavy or jagged anticlinal walls. The only other Rhaetian *Sphenobaiera* species in Jameson Land is *Sphenobaiera leptophylla* HARRIS 1935; it has much narrower leaf segments, an amphistomatic nature (albeit with slightly less stomata on the upper than on the lower cuticle) and straight anticlinal walls.

KELBER & VAN KONIJNENBURG-VAN CITTERT (1997) reported a ginkgoalean leaf fragment from Heilgersdorf as *Ginkgoites* sp., without describing or figuring it. No ginkgoalean remains have been recorded from Kipfen-dorf (ACHILLES 1981). *Ginkgoites taeniatus* (BRAUN) HARRIS 1935 is the only ginkgoalean species described from Wüstenwelsberg (VAN KONIJNENBURG-VAN CITTERT et al. 2021b). It differs in its much narrower segments, amphistomatic leaf anatomy and thinner cuticle.

Ginkgoites troedsonii LUNDBLAD 1959 was described by POTT & McLoughlin (2011) from the Rhaetian of Rögla (originally it was recorded from the Hettangian of Sweden only); it is only a leaf segment with a thick cuticle rather like the one described here but it differs in being amphistomatic and in its straight anticlinal walls of the epidermal cells. *Ginkgoites hermelinii* from the Hettangian of Jameson Land is also similar, especially in the macromorphology of some

Fig. 4. Cuticular remains of cycadophyte taxa from the Rhaetian of Einberg. **A** – *Pseudoctenis cteniforme*, cuticle fragment with indication of vein; from specimen O527/02. **B** – *Pseudoctenis cteniforme*, cuticle fragment with some stomata; from specimen O527/02. **C** – *Becklesia* sp., cuticle fragment showing overview with central stomatal free zone and remains of stomatal bands on either side; from cuticle slide 346. **D** – *Becklesia* sp., cuticle fragment with some papillae; from specimen 14Ei00. **E** – *Nilssonia* sp., thin cuticle fragment with stoma (inset); from specimen O506/01. **F** – *Pterophyllum zygotacticum*, overview of cuticle fragment; from specimen UU25969. **G** – *Pterophyllum zygotacticum*, one stoma; from specimen UU25969. **H** – Cycadophyte leaflet, cuticle fragment, arrow indicates hair base; from specimen O422/01. Scale bars equal 100 µm (A–F), H, 10 µm (G).

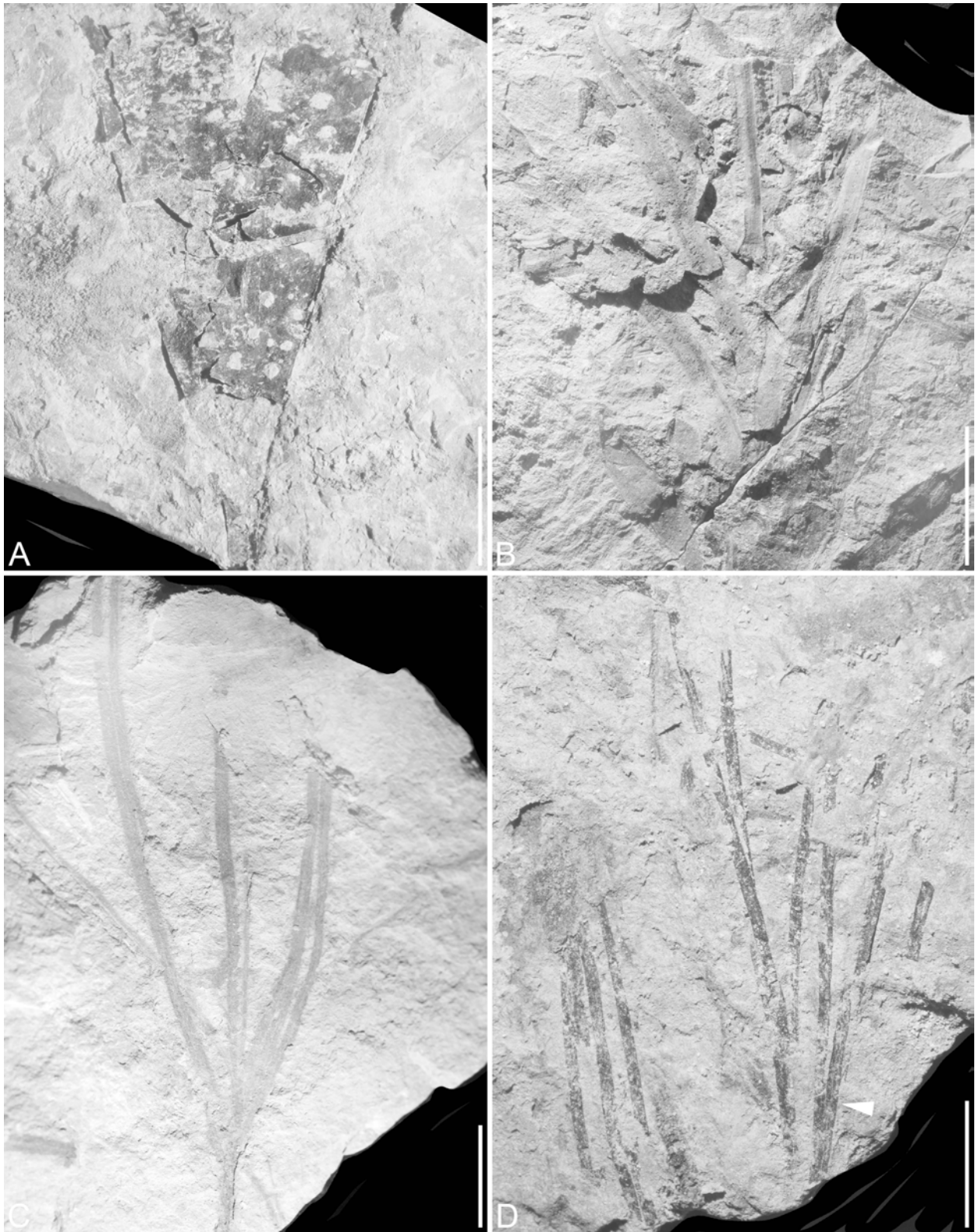


Fig. 5. *Sphenobaiera boeggildiana*, *Arberophyllum* sp. and *Czekanowskia nathorstii* from the Rhaetian of Einberg. **A** – *Sphenobaiera boeggildiana*, the only leaf fragment; 88Ei01. **B** – *Arberophyllum* sp., a bundle of six leaves; O551/02.

of the larger leaves, but these show a clear petiole that is absent in our specimen, and in fact represents the discriminating character of *Sphenobaiera* from *Baiera* and *Ginkgoites* (HARRIS 1935; FLORIN 1936). Moreover, the leaf substance of *Ginkgoites hermelinii* is thinner than that of *Sphenobaiera boeggildiana*, and the epidermal cells of the lower surface are only rarely papillate, whereas they are clearly papillate in *Sphenobaiera boeggildiana*.

The type species of *Sphenobaiera* (i.e., *Sphenobaiera spectabilis* (NATHORST) FLORIN 1936 from the Hettangian of Sweden, see also LUNDBLAD 1959) is a quite widespread species in the Hettangian, also occurring in several Hettangian localities in Bavaria (KRÄUSEL 1959; WEBER 1968) and Jameson Land (Greenland; HARRIS 1926; HARRIS 1935; HARRIS 1937). ASH & BASINGER (1991) and POTT et al. (pers. observation, January 2022) recorded the species also from the Rhaetian of Ellesmere Island, Arctic Canada, based on several specimens, alas without preserved cuticle remains. No similar material has yet been recorded from Poland (PACYNA 2014), the Donets Basin (STANISLAWSKI 1971) or Iran (SCHWEITZER & KIRCHNER 1995), at least no material in which cuticle remains were preserved that are necessary for a specific determination. ZHOU (1989) described *Sphenobaiera jugata* from the Rhaetian of Hunan (China), a species that is very similar both in macromorphology and cuticular anatomy to *Sphenobaiera boeggildiana*. The main difference is that in *Sphenobaiera jugata*, stomata may share subsidiary cells, while this has not been observed in *Sphenobaiera boeggildiana* so far, although stomata may be adjacent.

Occurrences in other adjacent Rhaetian floras: Jameson Land (East Greenland): HARRIS (1935, 1937).

Genus *Arberophyllum* DOWELD 2000

Arberophyllum sp.
Figs. 5B, 6D–G

Material studied: O551/02; cuticle slides without connected macro-specimen C. 297–300.

Description: On specimen O551/02 (Fig. 5B), a bundle of at least six leaves is preserved in a manner as if they were attached to a shoot, but the mode of attachment is not preserved. The longest of those leaf fragments is 35.0 mm long. The leaf width varies between 2.0 and 2.5 mm. The leaves appear to be longitudinally striate, and some are indicative of an indistinct depression or ridge in the middle of the lamina. The specimen yielded a thick cuticle reflecting an amphistomatic leaf anatomy with more stomata on the lower than on the upper side (Fig. 6D). Stomata are arranged in closely spaced rows with only a few rows of unspecified but papillate epidermal cells in between. Within a row, stomata are also closely spaced (Fig. 6E). Guard cells are sunken and rarely preserved, surrounded by 4–6 subsidiary cells that produce a solid papilla each, commonly overhanging the stomatal pit. There are four cuticle slides from similar leaves from bulk maceration (C. 297–300). These cuticles are identical with those of the specimen described above and we consider them conspecific (Figs. 6F, G).

Remarks: The generic name *Arberophyllum* is a substitute for the original generic name *Glossophyllum* KRÄUSEL 1943, because the latter name was already in use for a genus of extant mosses (see DOWELD 2000 for details). *Arberophyllum* is characterized by strap-like leaves with an entire margin and without a petiole. The leaves of the specimen from Einberg are much narrower (2.0–2.5 mm wide) than those of the type species *Arberophyllum florinii* (KRÄUSEL) DOWELD 2000 from the Carnian of Lunz (up to 15 mm wide), but its cuticle is very similar (POTT et al. 2007). Hence our attribution of the Einberg material to this genus, but we have too little material to make a specific assignment. Two *Arberophyllum* species are known from the Carnian of Svalbard (POTT 2014), viz., *Arberophyllum spetsbergensis* (VASILEVSKAYA) DOWELD 2000 and *Arberophyllum substrictum* POTT 2014. *Arberophyllum spetsbergensis* has leaves that are up to 19 mm wide in their central part, no cuticle has been described. The leaves of *Arberophyllum substrictum* are narrower (9–11 mm). The epidermal anatomy is only known from one specimen from Svalbard but is superficially similar to that of *Arberophyllum florinii* (POTT 2014) and the material from Einberg. No plant

C – *Czekanowskia nathorstii*, a bundle of eight leaves; O5/93. D – *Czekanowskia nathorstii*, remains of two leaf bundles with a possible bifurcation in one of them (see arrowhead); 10Ei01. Scale bars equal 10 mm.

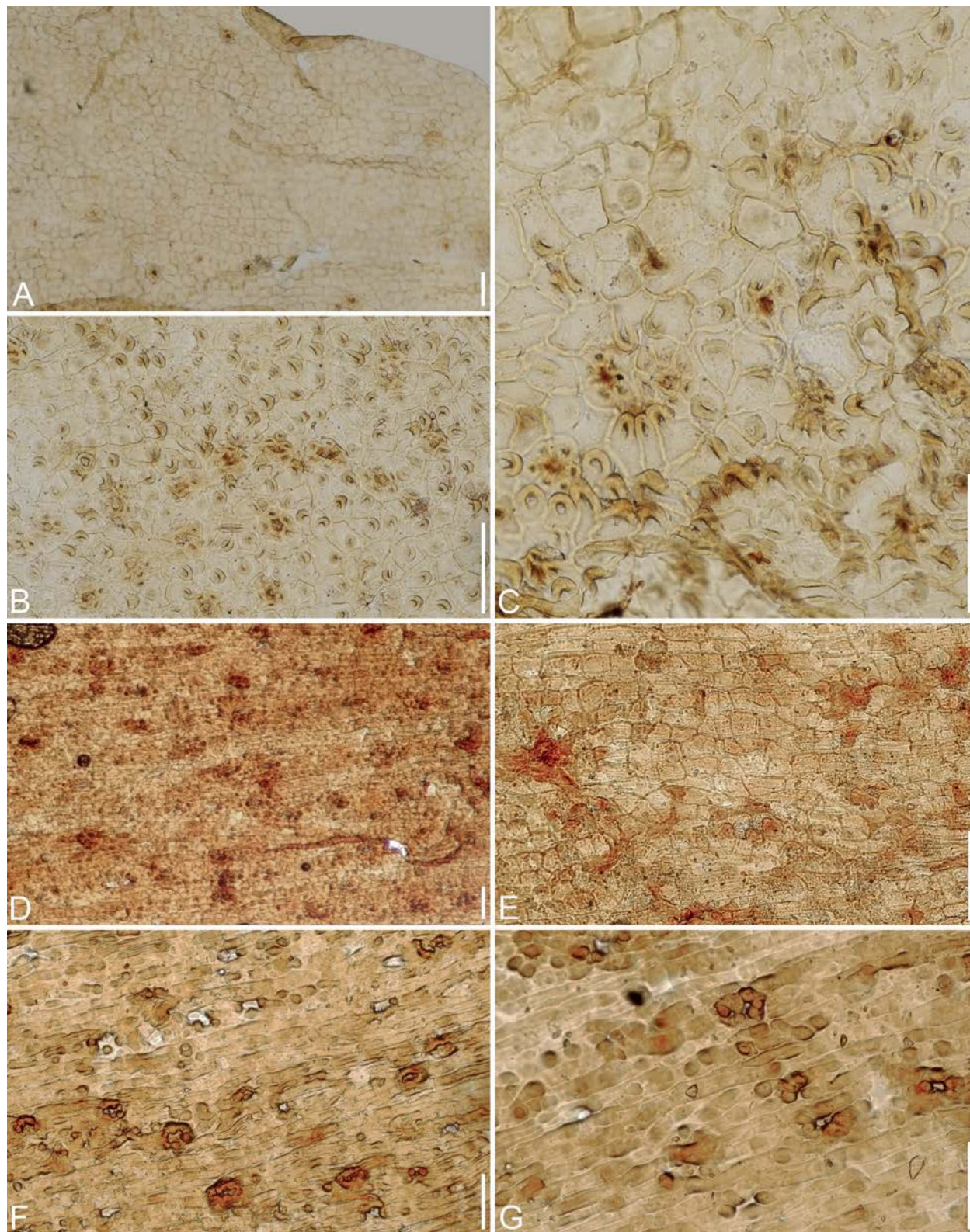


Fig. 6. Cuticular remains of ginkgophyte taxa from the Rhaetian of Einberg. **A** – *Sphenobaiera boeggildiana*, upper cuticle; from specimen 88Ei01. **B** – *Sphenobaiera boeggildiana*, lower cuticle from specimen 88Ei01. **C** – *Sphenobaiera boeggildiana*, detail of Fig. 6B showing stomata. **D** – *Arberophyllum* sp., lower cuticle fragment with rows of stomata; from spec-

fossils like the present specimens have been found in any Rhaetian locality around Coburg.

Order Czekanowskiales PANT 1957
Family Czekanowskiaceae SAMYLINA 1970
Genus *Czekanowskia* HEER 1876

Czekanowskia nathorstii HARRIS 1935
Figs. 5C, D, 7A–E

Synonymy:

- 1935 *Czekanowskia nathorstii* HARRIS, p. 40, pl. 4, figs. 3, 7, 9, pl. 5, figs. 1–5, pl. 6, figs. 2–4, 6–8, pl. 8 figs. 1, 2, text-fig. 19.
1937 *Czekanowskia nathorstii* HARRIS. – HARRIS, p. 58, no illustration.

Material studied: O5/93, 536/02, 550/02; cuticle slide without remaining specimen C.314; 10Ei01, 42Ei01, 59Ei01, 69Ei01, 75Ei01.

Description: Specimen O5/93 displays a bundle of eight leaves or leaf segments originating from a detached short shoot (Fig. 5C). All segments are c. 1.2 mm wide; the longest incomplete segment measures 75.0 mm. Cuticles could not be obtained from this specimen. 10Ei01 (Fig. 5D) is a specimen with two remains of detached leaf bundles bearing six and five leaf fragments, respectively. The longest fragment is 44 mm long and their width varies between 1.2 and 1.5 mm. None of the leaves appear to be bifurcate, although in one case, it is not clear if two leaves are laying above each other, or if it is one bifurcate leaf (Fig. 5D, arrow). A central vein is clearly visible in all leaves (Fig. 5D). Most other specimens are just leaf fragments with relatively thick cuticles that easily get dispersed; one of those (O536/02) yielded a cuticle fragment of a distinctly bifurcate leaf (Fig. 7C), 1.8 mm wide just below the bifurcation, with 1.2-mm-wide segments.

The cuticle is thick, reflecting amphistomatic leaves, with more stomata on the lower than on the upper surface. Epidermal cells have thick anticlinal walls, are commonly elongate, without papillae (Figs. 7A, B, D). The single vein is indicated by a few rows of more

elongate and narrower epidermal cells (Fig. 7D). Stomata are arranged in short rows (Figs. 7B, D). Guard cells are sunken; the 4–5 subsidiary cells are commonly slightly thickened (Fig. 7E). Just as HARRIS (1935: 41) wrote, the length of maceration time influences the aspect of the cuticles; “a densely staining layer becomes detached with longer maceration, disappearing more easily from the epidermal cells than from the subsidiary cells”. This appears to be typical for *Czekanowskia nathorstii*.

Remarks: HARRIS (1935) first described *Czekanowskia nathorstii* from the Hettangian and transitional beds (down to the Rhaetian) at Jameson Land including material described by NATHORST (1906) as *Czekanowskia rigida* and *Czekanowskia setacea* and by JOHANSSON (1922) as *Czekanowskia rigida* from Scania (Sweden). The specimens from Einberg perfectly agree with those of HARRIS (1935, 1937) in macromorphology and epidermal anatomy (including the mentioned effects of maceration time), with the exception that we found a central narrow zone of elongate epidermal cells without stomata, probably indicating the central vein. *Czekanowskia hartzii* HARRIS 1926 from the Hettangian of Jameson Land resembles *Czekanowskia nathorstii* but differs in having much narrower leaves (mean 0.7 mm wide) and a thinner cuticle with narrower and relatively more elongate epidermal cells (HARRIS 1935).

Foliate short shoots of *Czekanowskia* are traditionally macromorphologically subdivided into such with leaves with narrow segments (up to 1.5 mm, *Czekanowskia* ex gr. *rigida*) and those with leaves with wider segments (up to 5.0 mm wide, *Czekanowskia* ex gr. *latifolia*). Only when the cuticular anatomy is available, a more specific attribution can be made (SAMYLINA & KIRITCHKOVA 1993). Rhaetian species of *Czekanowskia* are relatively rare and often without preserved cuticular remains, and thus most have been described as *Czekanowskia* ex gr. *Czekanowskia rigida* (e.g., from Russia, see KRYSHTOFOVICH & PRINADA 1933, VOLYNETS & SHOROKOVA 2007, and Iran, see KILPPER 1971, SCHWEITZER & KIRCHNER 1995) or as *Czekanowskia* sp. (e.g., from Canada, see ASH & BASINGER 1991).

imen O551/02. E – *Arberophyllum* sp., detail of Fig. 6D showing stomata. F – *Arberophyllum* sp., lower cuticle fragment with rows of stomata, cuticle slide 297. G – *Arberophyllum* sp., detail of Fig. 6F showing stomata and papillate cells. Scale bars equal 100 µm.

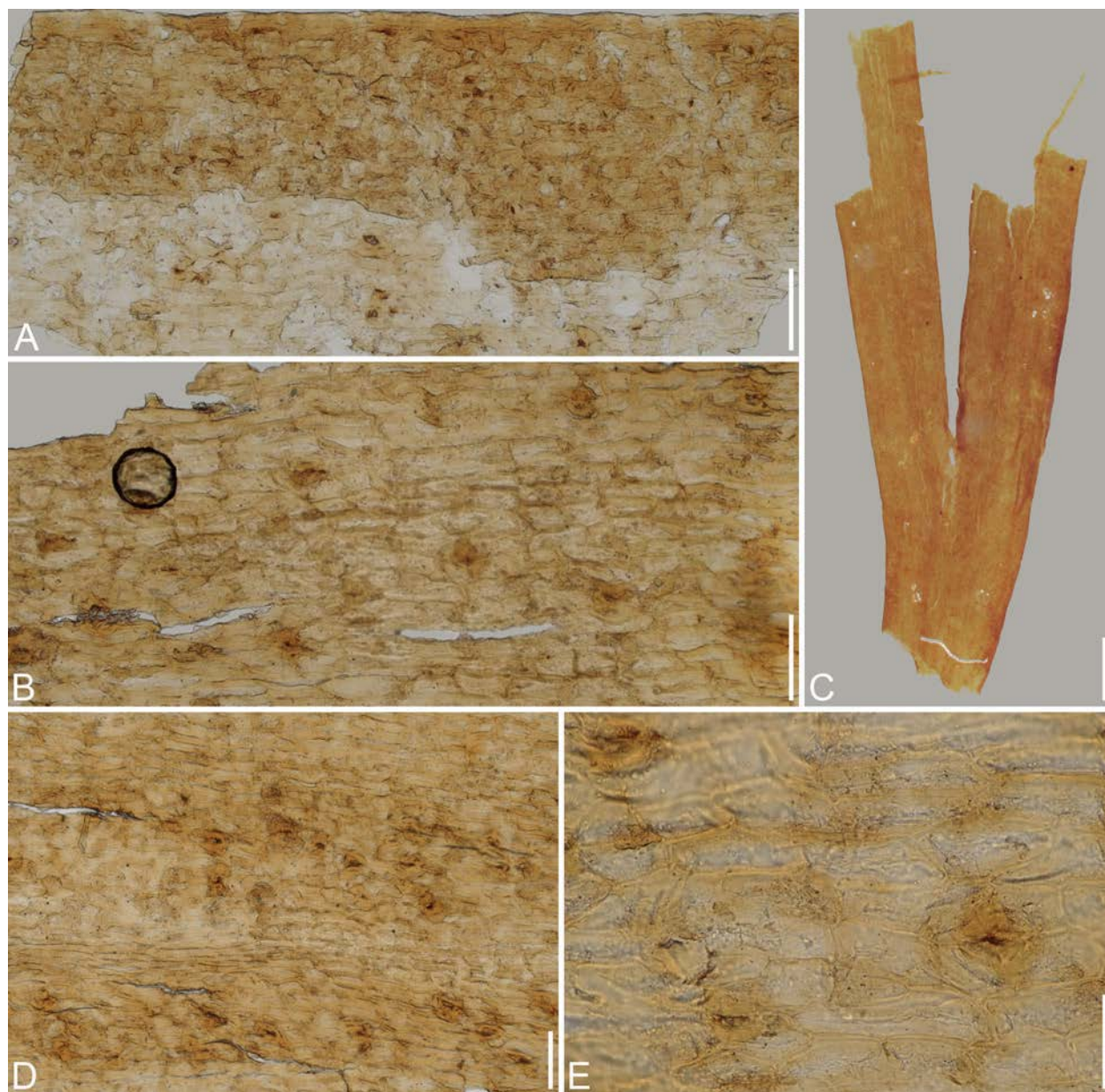


Fig. 7. Cuticular remains of *Czekanowskia nathorstii* from the Rhaetian of Einberg. **A** – Partly double cuticle; from specimen 10Ei01. **B** – Overview of a cuticle with stomatal row; from specimen O536/02. **C** – Bifurcate leaf; from specimen O536/02. **D** – Overview of a cuticle with two stomatal rows and indication of the vein; from specimen O536/02. **E** – Stomata; from specimen O536/02. Scale bars equal 1 mm (C), 100 μm (A, B, D), 50 μm (E).

The systematic position of the Czekanowskiales has yet to be resolved satisfyingly, although many authors consider the group closely related to the Ginkgoales, but some consider Czekanowskiales as a group of seed ferns (see, e.g., TAYLOR 1981). VAJDA et al. (2017, 2021) used cuticular infrared spectra and other “geochemical fingerprints” of Ginkgoales across the

Triassic-Jurassic boundary in Greenland, including *Czekanowskia nathorstii*, and compared them also with several seed fern and bennettitalean taxa from the same horizons. The authors concluded that Cycadales, Ginkgoales and Czekanowskiales formed one cluster, with Ginkgoales being the sister group of the Czekanowskiales. In contrast, Bennettitales were close-

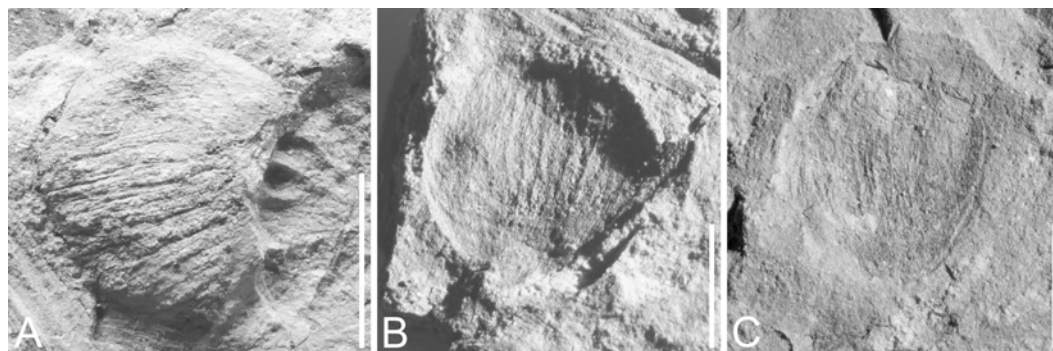


Fig. 8. *Leptostrobus* sp. from the Rhaetian of Einberg. **A** – *Leptostrobus* sp., showing a valve and on the right imprints of several seeds; O470/01. **B** – *Leptostrobus* sp., counterpart of Fig. 8A showing striate valve; O471/01. **C** – *Leptostrobus* sp., showing another dispersed valve; O473/01. Scale bars equal 5 mm.

ly linked with the Nilssoniales and some seed ferns (VAJDA *et al.* 2017; VAJDA *et al.* 2021), demonstrating a close alliance of Czekanowskiales and Ginkgoales.

Occurrences in other adjacent Rhaetian floras: Jameson Land (East Greenland): HARRIS (1935, 1937); Sweden: NATHORST (1906), ANTEVS (1919), JOHANSSON (1922).

Genus *Leptostrobus* HEER 1876

Leptostrobus sp.
Fig. 8A–C

Material studied: O470+471/01, O472+473/01, O474+475/01.

Description: Three specimens of detached *Leptostrobus* capsules have been encountered. O470/01 (and its counterpart O471/01; Fig. 8B) shows the outside of a capsule with a curved valve 9.1 mm high and up to 8.5 mm wide (just above the middle part) (Fig. 8A). The valve is curved and finely, longitudinally striate. The lower part of the valve is removed and thus the impressions of at least three ovules/seeds are visible (Fig. 8A). The base is incomplete, but the visible part is 1.5 mm wide. O472/01 (and its counterpart O473/01) shows another valve from the outside, again curved and finely striate; the height of the valve is 9.0 mm, but its base is missing (Fig. 8C). The width is up to 11 mm in the middle part and at the base 2.7 mm (but the ultimate part of the base is missing and might be slightly narrower). The margin of the valve is entire

and rounded. The third specimen is more incomplete but what is preserved agrees with the other two.

Remarks: Putative Czekanowskiales with reproductive organs have been recorded from the late Permian onwards (KUSTATSCHER *et al.* 2019), but records from the Jurassic and Cretaceous are much more numerous, whereas Triassic ones are rare (see, e.g., LIU *et al.* 2006). The female reproductive organs of various czekanowskialean genera are quite similar and commonly assigned to the genus *Leptostrobus*. Our material is, however, not well enough preserved to be assigned to a species. A *Leptostrobus* species was described from Jameson Land, viz. *Leptostrobus longus*, possibly belonging to the foliage *Czekanowskia hartzii* (HARRIS 1935). Other possible czekanowskialean reproductive organs that HARRIS (1935) described are *Staphiodora secunda* HARRIS 1935, attributed to *Hartzia tenuis* HARRIS 1935, and the enigmatic *Microcheiris enigma* HARRIS 1935. HARRIS (1951) stated that *Microcheiris enigma* is the valve of *Leptostrobus longus*, and that indeed *Staphiodora secunda* could be attributed to *Hartzia* and is quite similar to *Leptostrobus*. Our three specimens are not like those two species from Jameson Land, differing from *Leptostrobus longus* in their entire margin and from *Staphiodora secunda* in their much larger size (HARRIS 1935; HARRIS 1951). SCHWEITZER & KIRCHNER (1995) described *Leptostrobus laxiflora* from the Hettangian of Iran.

Other Late Triassic *Leptostrobus* species are known from floras much farther away, viz. cf. *Leptostrobus laxiflora* from the Rhaetian of Japan (ŌISHI & TAKAHASHI 1936), *Leptostrobus sphaericus* WANG *et al.* 1984 from the Late Triassic of China (LIU *et al.* 2006),

Leptostrobus cookii CLIFFORD et CAMILLERI 1998 from the Late Triassic of Queensland (Australia), and *Leptostrobus meyangamensis* KIM et al. 2002 from the Late Triassic of Korea, albeit with a subtending scale leaf, a feature that was never recorded before in the genus.

4. Discussion

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

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 cycadophytes and ginkgophytes. The flora is not as diverse as the assemblage recorded from another Rhaetian locality around Coburg, viz. Wüstenwelsberg (see Table 1; POTT et al. 2016; VAN KONIJNENBURG-VAN CITTERT et al. 2018; VAN KONIJNENBURG-VAN CITTERT et al. 2021a; VAN KONIJNENBURG-VAN CITTERT et al. 2021b), while it is much more diverse than the floras obtained from Kipfendorf (only one possible species in common, *Nilssonia* sp., but it is unclear if we are really dealing with the same taxon) and Heilgersdorf (also only one species possibly in common, *Pterophyllum aequale*).

None of the cycadophyte or ginkgophyte taxa described in this paper is common in the Einberg quarry. Most are only represented by a few specimens (*Pseudoctenis cteniforme*, *Nilssonia* sp., *Becklesia* sp., *Pterophyllum aequale*, *Pterophyllum zygoticum*, *Czekanowskia nathorstii*, and *Leptostrobus* sp.) or even only one (*Arberophyllum* sp. and *Sphenobaiera boeggildiana*). Some Einberg taxa were also recorded from Wüstenwelsberg (*Pseudoctenis cteniforme* and *Pterophyllum aequale*), the latter in a far lesser number of specimens than in Wüstenwelsberg (see Table 1; POTT et al. 2016, VAN KONIJNENBURG-VAN CITTERT et al. 2018), but *Pterophyllum zygoticum* has never been found at Wüstenwelsberg, just as the ginkgophytes *Sphenobaiera boeggildiana*, *Arberophyllum* sp., *Czekanowskia nathorstii* and *Leptostrobus* sp., while *Ginkgoites taeniatus* is quite common in the uppermost layers of Wüstenwelsberg but was not encountered in the Einberg assemblage so far (see Table 1).

Compared to other adjacent Rhaetian floras, the cycadophyte and ginkgophyte taxa from Einberg do not

have many species in common with those floras (Table 2). Einberg shares four taxa with Jameson Land (viz. *Pterophyllum aequale*, *Pterophyllum zygoticum*, *Sphenobaiera boeggildiana*, and *Czekanowskia nathorstii*), three with Scania (Sweden) (*Pseudoctenis cteniforme*, *Pterophyllum aequale* and *Czekanowskia nathorstii*), and only one (*Pterophyllum aequale*) with both Donets and Alborz (Table 2); none of the Einberg species has been found in southern Poland (PACYNA 2014). The other taxa from Einberg have had to be left in open nomenclature and can consequently not be compared with material from other areas.

The Einberg assemblage does not have one cycadophyte or ginkgophyte species in common with the Hettangian floras of Franconia (e.g., GOTHAN 1914; WEBER 1968).

4.2. Palaeoecological implications

A comparison with the other Rhaetian floras in species occurrences (Table 1) shows a difference in composition between the four localities around Coburg. This might reflect slightly different environments in which the plants lived or the fossil plants were embedded in these localities. 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 indicate the presence of moist environments with stagnant water bodies and/or small river systems in the Wüstenwelsberg area during the latest Rhaetian (VAN KONIJNENBURG-VAN CITTERT et al. 2020; VAN KONIJNENBURG-VAN CITTERT et al. 2021a).

Based on the composition of the flora so far reviewed, 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. Ongoing studies will target the conifers and will help to further characterise and refine the environment and habitats suggested for the area. 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 re-

Table 1. Occurrences of the various cycad, bennettitalean and ginkgoalean taxa at the four Rhaetian localities around Coburg, with their relative abundances.

	Taxon	Einberg	Wüstenwelsberg	Heilgersdorf	Kipfendorf
Cycadophytes	<i>Nilssonia pterophylloides</i>		X		
	<i>Nilssonia polymorpha</i>			?X	
	<i>Nilssonia</i> sp.	X			?X
	<i>Doratophyllum nathorstii</i>		X		
	<i>Ctenis latepinnata</i>		X		
	<i>Pseudoctenis florinii</i>		X		
	<i>Pseudoctenis cteniforme</i>	X	X		
	<i>Becklesia franconica</i>		X		
	<i>Becklesia</i> sp.	X			
	<i>Pterophyllum aequale</i>	X	X	?X	
	<i>Pterophyllum astartense</i>		X		
	<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>		X		
	<i>Wielandiella angustifolia</i>		X		
<i>Welsbergia bursigera</i>		X			
Ginkgophytes	<i>Ginkgoites taeniatus</i>		X		
	<i>Ginkgoites</i> sp.		X		
	<i>Sphenobaiera boeggildiana</i>	X			
	<i>Arberophyllum</i> sp.	X			
	<i>Czekanowskia nathorstii</i>	X			
	<i>Leptostrobus</i> sp.	X			

Table 2. Comparison of the cycadophyte and ginkgophyte taxa from Einberg to their presence in other adjacent Rhaetian floras.

Taxon	Einberg	Scania	Jameson Land	Donets	Alborz
<i>Nilssonia</i> sp.	X				
<i>Pseudoctenis cteniforme</i>	X	X			
<i>Becklesia</i> sp.	X				
<i>Pterophyllum aequale</i>	X	X	X	X	X
<i>Pterophyllum zygotacticum</i>	X		X		
<i>Sphenobaiera boeggildiana</i>	X		X		
<i>Arberophyllum</i> sp.	X				
<i>Czekanowskia nathorstii</i>	X	X	X		
<i>Leptostrobus</i> sp.	X				

lated 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). But these thin cuticles on the other hand may indicate that those plants commonly grew under moister circumstances. The only exception is *Sphenobaiera boeggildiana*, which has a relatively thick cuticle. The cuticle of *Czekanowskia nathorstii* is also distinctly thicker than that of the cycadophytes in

the assemblage. This might indicate that these species come from a slightly drier (more upland?) community and thus grew further away from the place of embedding, and leaves have been blown or washed in into the place where they have been embedded. When the third part of this assemblage (the conifer remains) has been described, there will be a general discussion on the size of specimens from individual plant groups (that varies considerably) from all four Rhaetian localities

in the Coburg area, possibly caused by adaptations to minor environmental and topographical conditions.

5. Concluding remarks

The Rhaetian flora of southern Germany is 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.

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