PalZ (2019) 93:531–541
https://doi.org/10.1007/s12542-019-00474-x

RESEARCH PAPER

A shoot with attached leaves of *Desmiophyllum harrisii* Barbacka et Pacyna from the Rhaetian of Bavaria, Germany

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Received: 11 July 2018 / Accepted: 30 May 2019 / Published online: 25 June 2019
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Abstract
Desmiophyllum harrisii was described from the Hettangian of Poland based on specimens yielding dispersed leaf fragments only, albeit with cuticle. Here, we record a shoot with attached leaves assignable to *Desmiophyllum harrisii* from the Rhaetian of Bavaria, besides a few specimens with dispersed leaf fragments. The leaves yielded also a thin and fragmentary cuticle with stomata arranged in characteristic single, short longitudinal files. This record does not only expand the temporal range of the species but also necessitates emending the specific diagnosis accordingly. The affinity of *Desmiophyllum* among gymnosperms is still uncertain, and the epidermal anatomy resembles that of Czekanowskiales and of some fossil taxa that have been assigned to Ginkgoales and Coniferales. The thin cuticle points to a habitat in moist environments.

Keywords Wüstenwelsberg · Rhaetian–Hettangian · *Desmiophyllum* · Czekanowskiales · Ginkgoales · Coniferales · Ecology

Introduction

The Rhaetian floras in the vicinity of Coburg, Bavaria, have recently received revived attention when the authors started with the description of the plant remains from a quarry at Wüstenwelsberg that proved to yield a highly diverse flora (see, e.g., van Konijnenburg-van Cittert et al. 2014, 2016, 2018; Pott et al. 2016a; and references therein). Another flora from the nearby quarry Einberg yet awaits examination, but is deemed much less diverse (personal observation of the authors). Preliminary determinations indicate the presence of *Lepidopteris* Schimper 1869 and *Peltaspermum* Harris 1937 and a considerable amount of conifer remains including cones.

During the course of the project and earlier collection activities, strap-shaped leaves and leaf fragments have repeatedly been found in the Rhaetian of Wüstenwelsberg and Einberg. Recently, a specimen was found among the earlier collected material from Wüstenwelsberg that, at the time, could not be attributed to any of the major plant groups found from that locality (viz. lycophytes, sphenophytes, seed ferns, cycads, bennettites and conifers). The specimen shows a shoot with strap-shaped leaves attached in a helical arrangement. Careful examination of the attached foliage, together with the preparation of fragile cuticle fragments,

Handling Editor: Benjamin Bomfleur.

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revealed that the specimen can be identified as *Desmiophyllum harrisii* Barbacka et Pacyna 2014, of which dispersed leaves have been described from the Hettangian of Poland by Barbacka et al. (2014).

Here, we describe this new specimen that necessitates emending the diagnosis of *Desmiophyllum harrisii* with the shoot characters. In addition, we could assign most of the isolated strap-shaped leaves and leaf fragments that had been collected at Wüstenwelsberg and Einberg to the same species. The material is compared with a few other species of *Desmiophyllum* Lesquereux 1878 in western European Rhaetian floras, and with other genera with strap-like leaves such as the czekanowskialean genus *Phoenicopsis* Heer 1876, the ginkgoalean genus *Arberophyllum* (Florin) Doweld 2000 and the genus *Pseudotorellia* Florin 1936, species of which are commonly assigned to either Ginkgoales or Coniferales, to discuss its systematic position.

Materials and methods

The Wüstenwelsberg sandstone quarry is situated approximately 20 km SW of Coburg, Germany (50°08′N/10°48′E; Fig. 1). The sediments were deposited in the Germanic Basin and are characterised by an alternation of clay and sandstone layers (for details see Bonis et al. 2010; Pott et al. 2016a; van Konijnenburg-van Cittert et al. 2018). The plant fossils come from the clay layers, one of which is the so-called Hauptton that can be up to 10 m thick. Almost all layers in the section are Rhaetian in age, except for the uppermost one (without any macrofossil remains, but with palynomorphs) that might be Hettangian in age (Bonis et al. 2010).

The discontinued quarry at Einberg is located outside the village of Rödental, 7 km ENE of Coburg (50°17′N; 11°03′E; Fig. 1). When sandstone production of the quarry ceased, it was filled with soil; the outcrops are consequently completely buried now and no longer accessible. Prior to that, plant fossils have been collected from small clay-lenses in the quarry.

The fossils used in this study originate from fieldtrips by some of the authors (SS, GD, JHAvKvC). The fossils are stored in the collections of the Laboratory of Palaeobotany and Palynology, University of Utrecht (the Netherlands; UU numbers) and in the private collections of Stefan Schmeissner (Kulmbach, Germany; numbers preceded by 'Q' for Wüstenwelsberg and 'O' for Einberg) and Günter Dütsch (Untersteinach, Germany; numbers containing the acronym 'wü' for Wüstenwelsberg). The plant fossil remains are preserved as compression fossils yielding cuticles.

Cuticles were picked directly from the rock surface. They were macerated according to the standard procedure (see Pott et al. 2016a) using Schulze's reagent (30% HNO_3 with a few crystals of $KClO_3$) and subsequently treated with 5–10% ammonia (NH_4OH) or potassium hydroxide (KOH). Macerated cuticles were rinsed with water and dehydrated in glycerine. The upper and lower cuticle surfaces were separated, embedded in glycerine jelly and sealed with transparent nail polish or paraplast. The slides are stored in the collection of the Laboratory of Palaeobotany and Palynology, Utrecht University, and in the private collections of SS and GD. The macrofossil specimens were photographed with a Panasonic DMC-FZ1000/Leica DC Vario-Elmarit 1:2.8–4.0/9.1–146 system digital camera. Cuticles were analysed with an Olympus BH2 light microscope.

Systematic description

Gymnospermae incertae sedis

Genus ***Desmiophyllum*** Lesquereux 1878 emend. Miller and Hickey 2010

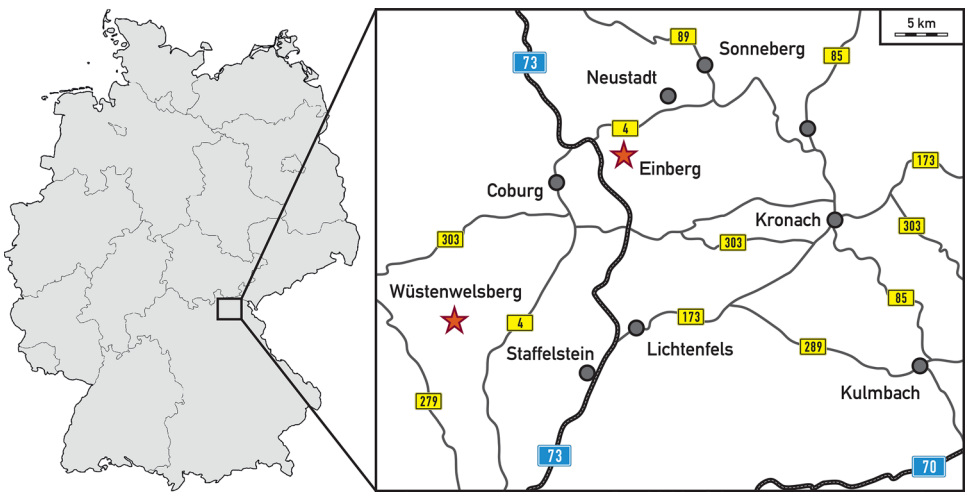

Fig. 1 Map of northeastern Bavaria showing the localities of Wüstenwelsberg and Einberg in the vicinity of Coburg

Type species. Desmiophyllum gracile Lesquereux 1878, from the Carboniferous (Pennsylvanian) of Cannelton, IN, USA.

Desmiophyllum harrisii Barbacka et Pacyna 2014, emend. Figures 2a–f, 3a–e

Reference.
2014 *Desmiophyllum harrisii*—Barbacka et al.: p. 300, pl. 9, figs. 6–8, text-figs. 3, 4.

Type. Holotype KRAM-P PM 139/100 (Palaeobotanical collection, W. Szafer Institute, Krakow, Poland).

Studied material. Q453/06 and its counterpart 04wü06, Q318/03, O140/98, O339/99, O407/01, O419/01, O420/01, UU25792, UU25968, UU26004, UU26010, UU26020.

Emended diagnosis. Strap-shaped leaves attached to a long shoot. Leaves long, linear. Veins parallel, 12–16 per/cm. Leaves hypostomatic, epidermal cells uniform on both lower and upper cuticle, elongate with straight cell walls. Stomata rare, sparsely arranged in irregular rows, longitudinally oriented; subsidiary cells commonly 4(–5) consisting of two polar and two or three long, slightly raised lateral subsidiary cells.

Description. Specimen Q453/06 (Fig. 2b) yields a c. 6 cm-long and 5 mm-wide shoot fragment, with 12 attached, strap-shaped leaves and some detached ones. The mode of attachment (phyllotaxis) cannot be recognized definitely, but appears to be helical. In all leaves, apices are not preserved, while the attached leaves show a slowly tapering base. The longest attached leaf fragment measures 9.6 cm, while the longest detached leaf fragment is 12 cm long. The width of the leaves varies between 3.5 and 5.1 mm. The venation consists of parallel veins that bifurcate near the leaf base. Vein concentration in the more distal part of the leaves is c. 12–16 veins/cm. Thinner veins or fibre strands can sometimes be seen between the veins (Fig. 2d, e, arrowheads).

The cuticle is very delicate; only small fragments were obtained after maceration revealing that the leaf is hypostomatic (Fig. 3). The lower and upper cuticles are equally thick. Epidermal cells are similar on both the upper and lower epidermis and are long with parallel longitudinal walls (Fig. 3a, b, e). They are up to 150 µm long and 5–20 µm wide. Stomata are sparsely distributed in irregular rows between the veins and orientated longitudinally (Fig. 3a, b, arrowheads). They consist of 4–5 subsidiary cells surrounding the guard cells: two even polar cells and usually slightly raised lateral cells (Fig. 3c, d).

The counterpart of Q453/06, i.e. 04wü06 (Fig. 2a), shows a cluster of leaves obscuring most of the shoot. The longest leaf fragment is 10.2 cm long and 4.9 mm wide. One leaf shows a clear bifurcation of veins in the basal part of the leaf. No cuticles could be prepared from the counterpart.

A single leaf fragment (Q318/03; Fig. 2c, e) shows a clear venation with distinct parallel veins; in one place, one of the indistinct veins can be observed as well (Fig. 2e, arrowhead). The small cuticle fragment of this specimen is identical with those from Q453/06. The few visible stomata have only four subsidiary cells, of which the two lateral ones were typically slightly raised above the level of the epidermis.

The Einberg material only contains leaf fragments. In some specimens, a number of several leaf fragments are preserved together. On specimen O407/01 (Fig. 2d, f), one 6-mm-wide leaf fragment has a very distinctly indicated venation clearly revealing the difference between the distinct and indistinct veins (Fig. 2d, arrowhead).

Remarks. The present material is identical with the detached leaves of *Desmiophyllum harrisii* as described by Barbacka and Pacyna (in Barbacka et al. 2014) from the Hettangian of Poland (compare, e.g., their pl. 9, figs. 6, 7 with our Fig. 2c, d). The Rhaetian material from Wüstenwelsberg additionally contains a shoot with a cluster of probably helically arranged leaves, necessitating the emendation of the specific diagnosis and adding to our knowledge of the species. Cuticles of the specimens from both localities are indistinguishable as well (compare, e.g., their pl. 9, fig. 8 and text-fig. 4 with our Fig. 3), but the Bavarian material yielded additional information on the arrangement of the stomata in short, irregular rows, due to larger and better preserved cuticle fragments (Fig. 3a, b).

Type locality and horizon. Huta OP-1 borehole, northern margin of the Holy Cross Mountains, Poland; Zagaje Formation, Huta Mudstone Member, Lower Hettangian, Jurassic.

Stratigraphic and geographic distribution. Rhaetian–Hettangian, Poland, Germany.

Discussion

Attribution of the specimens to *Desmiophyllum*

Desmiophyllum is a heterogeneous fossil-genus containing mainly elongate detached leaves with parallel venation. Epidermal anatomy of *Desmiophyllum* leaves is commonly unknown; it has been reported for only a few species until to date (see below).

The specimens reported here fit well in *Desmiophyllum* in the sense of the fossil-genus as emended by Miller and Hickey (2010). The elongate to lanceolate, linear to curvilinear leaves are simple, borne on long shoots and are

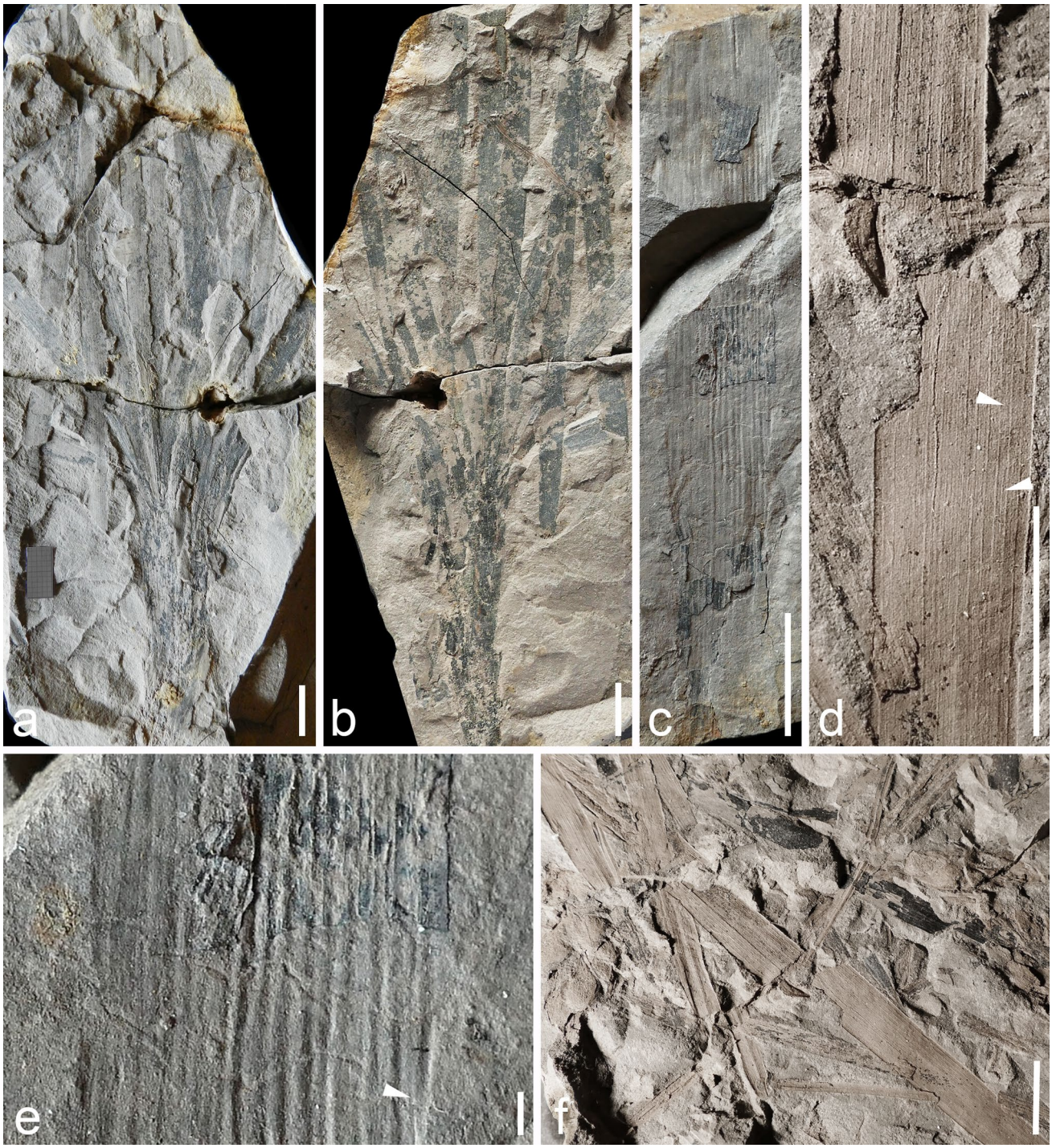

Fig. 2 *Desmiophyllum harrisii* Barbacka et Pacyna 2014, from the Rhaetian of Wüstenwelsberg (**a–c**, **e**) and Einberg (**d**, **f**), Bavaria, Germany. **a** Specimen 04wü06 showing a shoot with several attached strap-shaped leaves. **b** Specimen Q453-06, counterpart to the specimen in **a**. **c** Specimen Q318-03 showing a single leaf with organic matter preserved, note the fine venation. **d** Specimen O407-01, detail of **f**, depicting the position of thinner veins (arrowheads) between the more prominent veins. **e** Detail of **c**, showing the fine venation (arrowhead). **f** Specimen O407-01 with several detached leaves scattered on the surface. Scale bars 1 cm (**a–d**, **f**), 1 mm (**e**)

commonly interpreted deciduous as they are almost always found detached, but some authors interpreted the leaves as persistent (Miller and Hickey 2010). The leaf base is commonly contracted, the apex acute to obtuse, the margins entire. The veins are distinct (to sometimes indistinct), subparallel to parallel, forked near the leaf base (or occasionally without forking) and converging towards the apex. The epidermis is characterized by haplocheilic stomata.

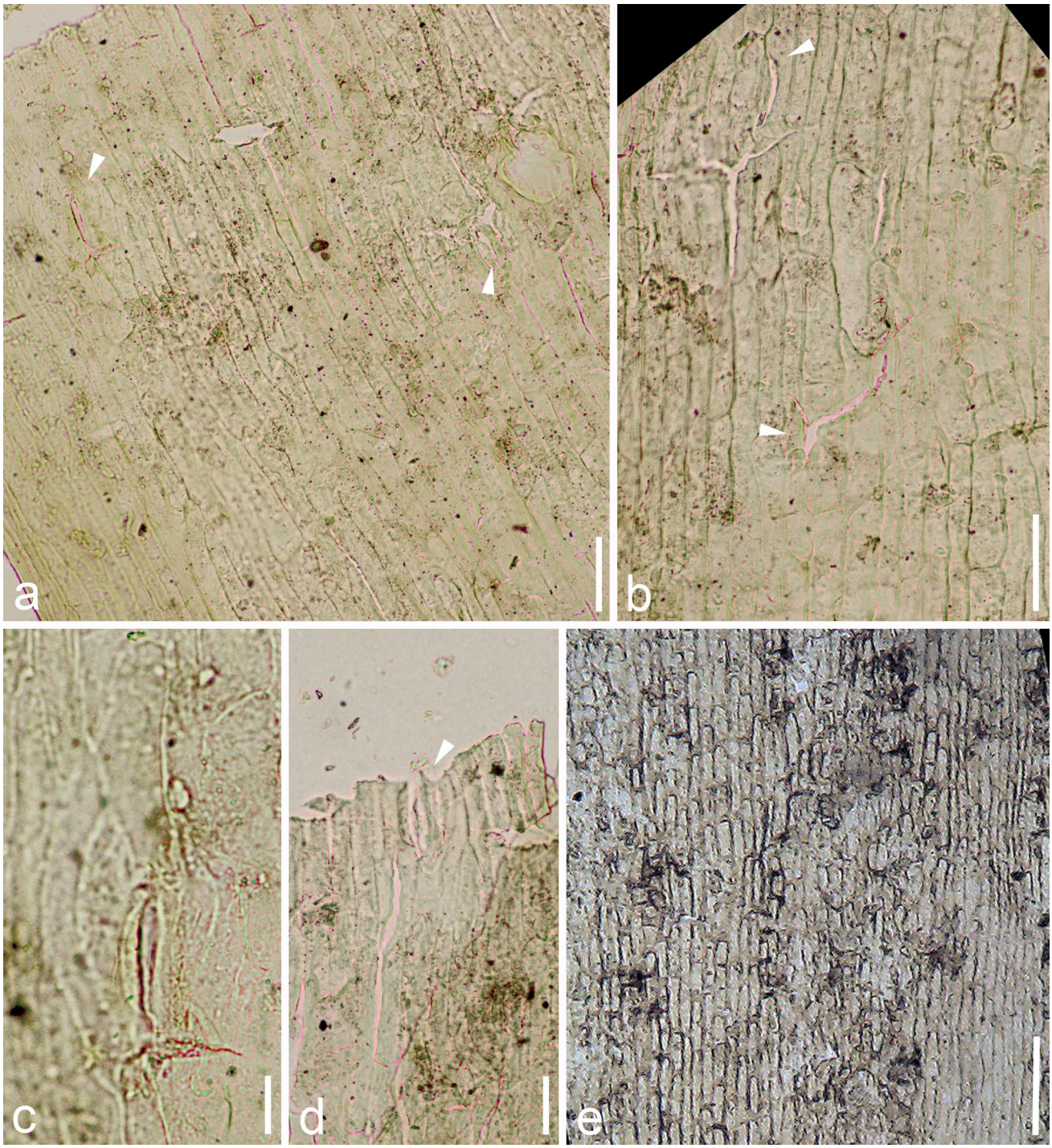

Fig. 3 Cuticle of *Desmiophyllum harrisii* Barbacka et Pacyna 2014, from the Rhaetian of Wüstenwelsberg (**a–d**, specimen Q453-06) and Einberg (**e**, specimen O399-99), Bavaria, Germany. **a** Overview of lower cuticle with stomata (arrowheads). **b** Detailed view of lower cuticle with two stomata depicted by arrowheads. **c, d** Close-ups of two different stomata showing the slightly raised lateral subsidiary cells and a hint of the guard cells (in **d**). **e** Overview of upper cuticle. *Scale bars* 100 µm (**a**, **b**, **e**), 20 µm (**d**), 10 µm (**c**)

Desmiophyllum is designed specifically to be used as a 'fossil-genus' for poorly known material, so it certainly has more than one 'botanical affinity', and if any of these can be clarified for any species, then that species will likely be transferred to a different genus such as the conifer genera *Podozamites* Braun 1843 and *Pityophyllum* (Nathorst 1879)

Seward 1919, the presumed ginkgoalean genus *Arberophyllum* Doweld 2000 (a substitute for *Glossophyllum* Kräusel 1943; Doweld 2000; Pott 2014), the czekanowskialean genera *Phoenicopsis* and *Arctobaiera* Florin 1936, or the ginkgoalean/coniferalean genera *Pseudotorellia* or *Torellia* Heer 1870. All these genera comprising long and strap-shaped leaves are comparatively similar in their features and consequently difficult to distinguish (see Table 1). Some are borne on short shoots that might or might not be shed as a whole, while others are borne on long shoots and shed individually.

The leaves under study here are long and strap-shaped, borne on a long shoot, their base is tapering while the apex is yet unknown. The venation is delicate and parallel; veins are bifurcating once close to the rachis. The cuticle is thin, and the leaves are hypostomatic, stomata are elongate (oval) and oriented strictly longitudinally. A synopsis of the features of the genera under discussion (Table 1) reveals that the leaves under study here are at best placed in *Desmiophyllum*. An assignment to *Arberophyllum* is not warranted as *Arberophyllum* requires amphistomatic leaves and randomly oriented stomata (Pott 2014). From the other genera, the leaves here assigned to *Desmiophyllum harrisii* are distinguished either by their arrangement on long shoots in contrast to the short-shoot arrangement in, e.g., *Phoenicopsis* or *Pseudotorellia*, or by details in epidermal anatomy, mainly arrangement and longitudinal vs. random or transverse orientation of the stomata as in *Podozamites*, whereas *Arctobaiera* is distinguished by the commonly bi-lobed leaf apex and *Pityophyllum* has, similar to *Czekanowskia*, single-veined needle-like leaves (Table 1).

Comparison with other Triassic/Lower Jurassic *Desmiophyllum* species

There are only a few definitely circumscribed Late Triassic (Carnian–Rhaetian) and Early Jurassic (Hettangian) *Desmiophyllum* species from European localities although there are a larger number of plant remains that have been left unassigned as *Desmiophyllum* sp. (see, e.g., Dobruskina 1994). The leaves of *Desmiophyllum variabile* Vasilevskaya 1985 (from the Carnian of Novaya Zemlja, Russia) are a much wider (up to 27 mm) with a truncate base and unknown cuticle, while the leaves of another Carnian species, viz. *Desmiophyllum imhoffii* Florin 1936 (from Neuewelt, Basel, Switzerland) are also much wider and appear more robust. They can show a typical rhombic structure when the epidermis is missing through erosion (Kelber and Hansch 1995); this taphonomic feature has so far only been encountered in that species.

Desmiophyllum acuminatum Stanislavsky 1976 from the Norian of the Donets Basin (Ukraine) is commonly found as detached leaves of similar shape as *Desmiophyllum harrisii*, but with a higher vein density. Epidermal anatomy is also unknown in this species. *Desmiophyllum cyclostomum* from the Rhaetian of Scania, Sweden, attributed to the Cycadales because of the similarity of the stomata with those of *Bjuvia* Florin 1933 by, e.g., Lundblad (1959) and Pott and McLoughlin (2011), is also wider (up to 29 mm) than *Desmiophyllum harrisii*, but the main difference is recognised in the cuticle that is much thicker than in *Desmiophyllum harrisii*. Epidermal cells are isodiametric to polygonal and the stomata are randomly scattered. The subsidiary cells around the stomatal pit have raised margins resulting in a continuous circular ridge around the stomatal pit (Pott and McLoughlin 2011). *Desmiophyllum gothanii* Florin 1936 has also much wider leaves (up to 20 mm) than *Desmiophyllum harrisii*, and the cuticle is thicker with more and more pronounced rows of stomata (Florin 1936; pers. obs. JHAvK-vC). *Desmiophyllum gothanii* was, in addition, found in association with reproductive structures of unknown gymnosperm affinity such as the microsporangiate reproductive organ *Piroconites kuespertii* Gothan 1914 and the seed cone *Bernettia inopinata* Gothan 1914 (see, e.g., Kustatscher et al. 2016).

Harris (1935) recorded three *Desmiophyllum* species from the Rhaetian–Hettangian of Jameson Land (Greenland). The leaves of the Hettangian *Desmiophyllum* sp. 1 are narrower than *Desmiophyllum harrisii* (only 1.5 mm wide) with only 1–2 veins, and no cuticle is known—it remains ambiguous whether these are in fact *Desmiophyllum* leaves. *Desmiophyllum* sp. 2 (also Hettangian in age) is very similar in morphology to *Desmiophyllum harrisii*, but no cuticle could be prepared from the specimens. Later, Harris (1946) figured new specimens of *Desmiophyllum* sp. 2 and added to the original description only that the leaves might indeed have been 20–30 cm long. Even later, Harris and Miller in Harris et al. (1974) placed it as cf. in the synonymy of *Desmiophyllum gramineum* Harris et Miller 1974, a species erected based on material from the Bajocian of Yorkshire, UK, because it also had long leaves with a similar venation and a cuticle 'impossible to prepare' (Harris et al. 1974: p. 138), although the authors were able to prepare cuticle pieces from the Yorkshire material. *Desmiophyllum gramineum* is rather similar to *D. harrisii*, but differs in its slightly narrower leaves (3–4 mm wide) and lower vein density (6–10 per cm) and its amphistomatic nature of the leaves. Barbacka et al. (2014) placed *Desmiophyllum* sp. 2 in the synonymy of *Desmiophyllum harrisii*. However, as long as no cuticle has been recovered, we refrain from definitely determining the material from Jameson Land as such. The Rhaetian *Desmiophyllum* sp. 3 was initially described by Harris (1926) as '?*Podozamites* sp. A' and later corrected into *Desmiophyllum* sp. 3 (Harris 1935). The single leaf fragment is 16.5 cm long and 12.5 mm wide in the middle, thus being considerably wider than *Desmiophyllum harrisii*. No cuticle is known of this species.

Table 1 Comparison between genera with strap-like leaves

Genus	Possible affinity	Long/short shoots	Leaf shape	Base/apex	Venation	Cuticle thickness stomatal arrangement	Stomatal shape and orientation
Desmiophyllum	gymnosperm, possibly Ginkgoales or Czekanowskiales	Long shoot	Long, strap-shaped	Tapering base apex acute-obtuse	Parallel, veins forked near leaf base	Thin hypostomatic in single files	Shape elongate, longitudinally orientated
Arberophyllum	Ginkgophytes	Long shoot	Long, strap-shaped	Tapering base apex obtuse	Parallel, veins forked near leaf base	Thin–thick amphistomatic in files within stomatal bands	Shape more circular, random orientation
Phoenicopsis	Czekanowskiales	Short shoot	Long, strap-shaped	Slightly tapering base apex acute-obtuse	Parallel, veins occasionally forking	Thick hypostomatic or amphistomatic in single files	Shape elongate, longitudinally orientated
Arctobaiera	Czekanowskiales	Long and short shoots	Long, strap-shaped	Slightly tapering base apex obtuse, or divided into 2 lobes	Parallel, veins forked near leaf margin	Thick hypostomatic or amphistomatic in files within stomatal bands	Various shapes predominantly longitudinally orientated
Pseudotorellia	Ginkgoales or Conifers	Short shoot	Strap- to tongue-shaped	Tapering base apex obtuse	Parallel, veins forked near leaf base	Thick commonly hypostomatic, in files, in stomatal bands	Various shapes longitudinally orientated
Podozamites	Conifers	Restricted long shoots	Tongue- to slightly strap-shaped	Constricted base apex obtuse	Parallel, veins forked near leaf base	Thin hypostomatic, in files, in stomatal bands	Transversely orientated
Pityophyllum	Conifers	Long and short shoots	Long, needle-shaped	Tapering base apex acute	Single-veined	Thin imperfectly known	Imperfectly known

Data are based on Harris (1935), Zhou and Zhang (1996), Miller and Hickey (2010), Nosova and Kiritchkova (2011), Pott (2014), Huang et al. (2016), Nosova and Golovneva (2018), Shi et al. (2018), and the present paper

Comparison with similar *Pseudotorellia* species

A genus that accommodates very similar leaves is *Pseudotorellia*, instituted by Florin (1936) to host strap- to tongue-shaped leaves with a leathery (coriaceous) appearance with basally bifurcating parallel veins. Leaves are commonly hypostomatic with haplocheilic stomata arranged in short longitudinal bands between veins on the lower epidermis (see Watson and Harrison 1998; Pott et al. 2016b and Shi et al. 2018 for a more detailed discussion of *Pseudotorellia*), but one species, *Pseudotorellia amphistomatica*, from the Cretaceous of Siberia has amphistomatic leaves (Golovneva and Nosova 2012). If the leaves under study here had a coriaceous appearance, they also fitted in *Pseudotorellia*, especially, if different species such as *Pseudotorellia nordenskioeldii* (Nathorst) Florin 1936 or *Pseudotorellia longifolia* Doludenko in Vakhrameev et Doludenko 1961 are considered (see below).

Pseudotorellia is traditionally regarded as a ginkgoalean species (see, e.g., Pott et al. 2016b). However, this affinity has been challenged repeatedly. Watson and Harrison (1998) showed in an elaborate study that shoots of *Abietites linkii* (Roemer) Dunker 1846, long since regarded as coniferous, and leaves of *Pseudotorellia heterophylla* Watson 1969 and the coniferous *Pityophyllum crassum* Seward 1926, are portions of one and the same natural species, *Pseudotorellia linkii* (Roemer) Watson et Harrison 1998. However, the authors could not solve the then emerging dilemma: the question of the systematic position of *Pseudotorellia linkii* is still problematical and remains far from conclusive in the light of the associated shoots, which have now been shown to bear what have hitherto been regarded as undoubted ginkgoalean leaves. Shi et al. (2018) also discussed the systematic position of *Pseudotorellia* based on an elaborate cuticular study of *Podozamites* (commonly referred to conifers) and *Pseudotorellia* leaves, but also came to no convincing conclusion regarding the position of *Pseudotorellia*.

Rhaetian *Pseudotorellia* species that are similar to the leaves here assigned to *Desmiophyllum harrisii*, but remain still distinguishable include *Pseudotorellia ephela* (Harris 1935) Florin 1936 from Greenland (Harris 1935) that has very similar stomata to *Desmiophyllum harrisii* (cf. Harris 1935: text-fig. 21), but its shorter leaves (complete leaves 2–8 cm long) with their rounded apices clearly distinguish it from *Desmiophyllum harrisii*, and *Pseudotorellia minuta* Lundblad 1957, which has strongly papillate stomata discriminating it clearly from *Desmiophyllum harrisii*.

The following species derive from much younger deposits (Jurassic–Cretaceous), but since there are obvious similarities to *Desmiophyllum harrisii*, they are considered in brief here as well. *Pseudotorellia nordenskioeldii* from Svalbard, Norway, is almost identical from its macroscopic and microscopic features though known leaves are only up to 44 mm long (Pott et al. 2016b) and stomata, especially the subsidiary cells, are different in shape, arrangement and cutinisation of the stomata. A little longer (viz. c. 90 mm) by a more or less similar width are the leaves of *Pseudotorellia longifolia* (3–5 mm wide), *Pseudotorellia ensiformis* (Heer) Doludenko in Vakhrameev et Doludenko 1961 (up to 6–10 mm wide) and *Pseudotorellia angustifolia* Doludenko in Vakhrameev et Doludenko 1961 (up to 3 mm wide) from the Bureja Basin, in which also the epidermal anatomies approach that of *Desmiophyllum harrisii* (Vakhrameev and Doludenko 1961; see also Pott et al. 2016b). Although the stomata are similar, the cuticles are thicker and the stomata are more densely arranged in the irregular rows. Some but less epidermal similarity is also seen in the various *Pseudotorellia* species erected by Nosova and Golovneva (2018) and Shi et al. (2018) from Western Siberia and Mongolia. *Pseudotorellia heeri* Manum 1968 from Svalbard also shows agreement in macroscopic and epidermal anatomy (Manum 1968). Although there are obvious similarities of the different *Pseudotorellia* species to *Desmiophyllum harrisii*, we refrain from assigning the leaves and shoots under study to *Pseudotorellia* as especially evidence in epidermal anatomy and leaf appearance (entire leaf length; coriaceous—generally involving a thick cuticle, and Lundblad (1968) for example rejected all species from *Pseudotorellia*, where epidermal anatomy is unknown) is not sufficient for ultimate assignment; in addition, the systematic position of *Pseudotorellia* is still ambiguous.

Comparison with selected *Phoenicopsis* species

The czekanowskialean genus *Phoenicopsis* contains leaves attached in bundles to caduceus, that is deciduous, spur shoots in a similar manner as in Ginkgoales; some authors, therefore, regarded both orders as closely related (e.g., Harris 1935; Schweitzer and Kirchner 1995). The leaves are commonly fitted with robust cuticles and can be hypostomatic or amphistomatic; stomata are placed in single longitudinal rows (sometimes rows arranged in bands) and are commonly elongate with two polar and 2–4 lateral subsidiary cells such as in *Desmiophyllum harrisii*. However, both epidermal and subsidiary cells are often papillate in *Phoenicopsis*.

Phoenicopsis seems to have occurred mainly in Asia. The genus was erected based on fossils from the Middle Jurassic of the Upper Amur (Manchuria, Heer 1876); the majority of species has been also recorded from Russia (from the Carnian onwards, see, e.g., Dobruskina 1994; Volynets and Shorokhova 2007). Outside Russia, there are records from China and Japan (Kimura et al. 1988; Sun et al. 2015; Huang et al. 2016; Pott and Jiang 2017) and Kazakhstan and Iran (Nosova and Kiritchkova 2011 and references therein). A few Jurassic species are known from Europe, e.g., from

Poland (Barbacka et al. 2014), Romania (Barbacka et al. 2015) and Scotland (van Konijnenburg-van Cittert and van der Burgh 1989).

One of the two *Phoenicopsis* species that have a cuticle fairly similar to that of *Desmiophyllum harrisii* is the Middle–Late Jurassic *Phoenicopsis daohugouensis* Huang et al. 2016 with 3–4 mm wide amphistomatic leaves that have stomata similar to those of *Desmiophyllum harrisii*, but with sometimes papillate subsidiary cells. The second one that shows cuticular similarity, especially in the anatomy of the stomata, is the Lower Cretaceous species *Phoenicopsis papulosa* Samylina 1983 (Nosova and Golovneva 2018), but it differs in having papillate subsidiary cells. Moreover, the stomata are arranged in stomatal bands (albeit in distinct single files within those bands) and the anticlinal walls of the epidermal cells of the upper cuticle are sinuous.

Ecological remarks

Desmiophyllum harrisii is found in Bavaria in clay lenses in sandpits, 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 *Desmiophyllum harrisii* with completely unprotected stomata that are even with the epidermis surface can be interpreted as the plant thrived in a moist environment. However, 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 and McLoughlin 2009; Bonis et al. 2010) such as, e.g., in Jameson Land, Scania and Wüstenwelsberg. At the latter, this is supported by a palynomorph spike of horsetail, lycophyte and fern spores, and remains of aquatic algal cysts (Bonis et al. 2010). This also indicates that stagnant or slowly running water bodies existed in the Wüstenwelsberg area during the latest Rhaetian (van Konijnenburg-van Cittert et al. 2014, 2016; Pott et al. 2016a). This is, moreover, supported by the overall composition of a diverse and abundant flora, rich in hygrophytic elements, which in many cases are dependent on the presence of liquid water for their reproduction cycles. Besides deltaic or moist environment-related and fresh water-dependent plant groups, such as the spore-reproducing club mosses, horsetails and ferns (van Konijnenburg-van Cittert et al. 2016, 2017, 2018), a high number of bennettitalean taxa are present in the flora (Pott et al. 2016a). Bennettitaleans are seed plants that are interpreted to have thrived predominantly in deltaic and highly disturbed environments (see, e.g., Pott and McLoughlin 2009, 2014; Pott et al. 2016a). A similar scenario has been interpreted for most of the cycads recorded from Wüstenwelsberg (van Konijnenburg-van Cittert et al. 2018). In the palynological profile of Wüstenwelsberg (Bonis et al. 2010), no marine elements have been recorded, and hence a fresh water environment is favoured. For a further and more detailed interpretation of the environment and habitats, in which the Wüstenwelsberg flora thrived, see van Konijnenburg-van Cittert et al. (2014, 2016, 2018) and Pott et al. (2016a). In Poland, *Desmiophyllum harrisii* appeared in a similar environment that is interpreted as lacustrine—in a fern-gymnosperm-dominated community (Barbacka et al. 2014), while Harris (1937) recorded it from deltaic river settings in East Greenland. Consequently, *Desmiophyllum harrisii* can be regarded as a plant thriving in moisture-related environments commonly along slow-running or standing water bodies.

Acknowledgements The authors wish to thank Fabian Ercan (University of Utrecht) with his help with the cuticle photos. Thanks are also due to Gea Zijlstra (University of Utrecht) for her help in nomenclatorial issues. Constructive comments from Majka Barbacka, Benjamin Bomfleur and Natalja Nosova helped to improve the paper.

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