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Bennettitales in the Rhaetian flora of Wüstenwelsberg, Bavaria, Germany

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A B S T R A C T

The diverse bennettitalean plant remains from the Rhaetian of Wüstenwelsberg, Franconia, southern Germany, are described by means of macromorphological and epidermal anatomy; the study is part of the ongoing examination of this recently excavated and excellently preserved fossil flora. The taxa identified include four species of *Pterophyllum*, one species of *Anomozamites*, two species of *Nilssoniopteris* and one species of *Wielandiella* with sterile leaves, bracts and ovulate reproductive organs. In addition, an enigmatic type of bennettitalean microsporangiate organ has been obtained, remains of which from the Rhaetian of Greenland had been assigned to *Bennettistemon*. However, the material from Wüstenwelsberg is much more complete and is assigned to a new genus, viz. *Welsbergia* gen. nov., with its type species *Welsbergia bursigera* (Harris) comb. nov., based on the organ's unique architecture. The microsporangiate organs are always exclusively associated with the sterile foliage *Pterophyllum aequale*. Comparison of the flora from Wüstenwelsberg with adjacent Rhaetian floras revealed distinct local differences in the bennettitalean constitution, which are discussed in the light of palaeogeography and plant dispersal patterns.

1. Introduction

The fossil flora from the uppermost Triassic and the Lower Jurassic of Upper Franconia (Bavaria, Germany), more widely known as the “Rhaeto-Liassic flora” of Upper Franconia, has received considerable scholarly attention (for references see Van Konijnenburg-van Cittert et al., 2014). Most of the localities expose Hettangian (Lower Jurassic) strata and are distributed extensively around the towns of Bayreuth and Nürnberg (see, e.g., Gothan, 1914). However, a few localities around the town of Coburg host Rhaetian (Upper Triassic) assemblages (see, e.g., Kelber and Van Konijnenburg-van Cittert, 1997; Van Konijnenburg-van Cittert et al., 2014). One of these is a quarry near the village of Wüstenwelsberg (Fig. 1). During recent decades, systematic sampling yielded over 40 species of fossil plants from this quarry; this is a much larger number than in, for example, the nearby locality Heilgersdorf (Kelber and Van Konijnenburg-van Cittert, 1997). The flora of Wüstenwelsberg is currently under thorough study, and several species and taxa have been described by Bonis et al. (2010), Zavialova and Van Konijnenburg-van Cittert (2011) and Van Konijnenburg-van Cittert et al. (2014, 2016).

In this paper, we describe the diverse Bennettitales, one of the dominant groups in the Wüstenwelsberg flora. We have identified one species of the fossil genus *Anomozamites*, four species of *Pterophyllum* and two species of *Nilssoniopteris*. Besides these isolated foliage types, leaves of *Wielandiella angustifolia* (earlier known as *Anomozamites angustifolius*; see Pott, 2014a) have been found, accompanied by isolated scale leaves of its ovulate reproductive organs and one compressed ovulate organ. Finally, we identified well-preserved specimens of *Bennettistemon bursigerum*, which has recently been argued to be the possible male reproductive organ of *W. angustifolia* (Pott, 2014a), but which is always associated with *Pterophyllum aequale* in our assemblage. These specimens of *B. bursigerum* strongly expanded our knowledge of this species warranting its transferal to another genus, viz. *Welsbergia* gen. nov., which is here erected for this type of bennettitalean microsporophyll with its type species *Welsbergia bursigera* comb. nov.

The ecology and habitat of the parent vegetation are discussed with focus on the dominant bennettitalean plants. In addition, we compare the composition of this flora to that of other Rhaetian and Hettangian assemblages, such as those from East Greenland (Jameson Land), Sweden (Scania), Poland, Hungary (Mecsek Mountains) and Ukraine (Donets Basin), and discuss potential biogeographic relationships and dispersal patterns.

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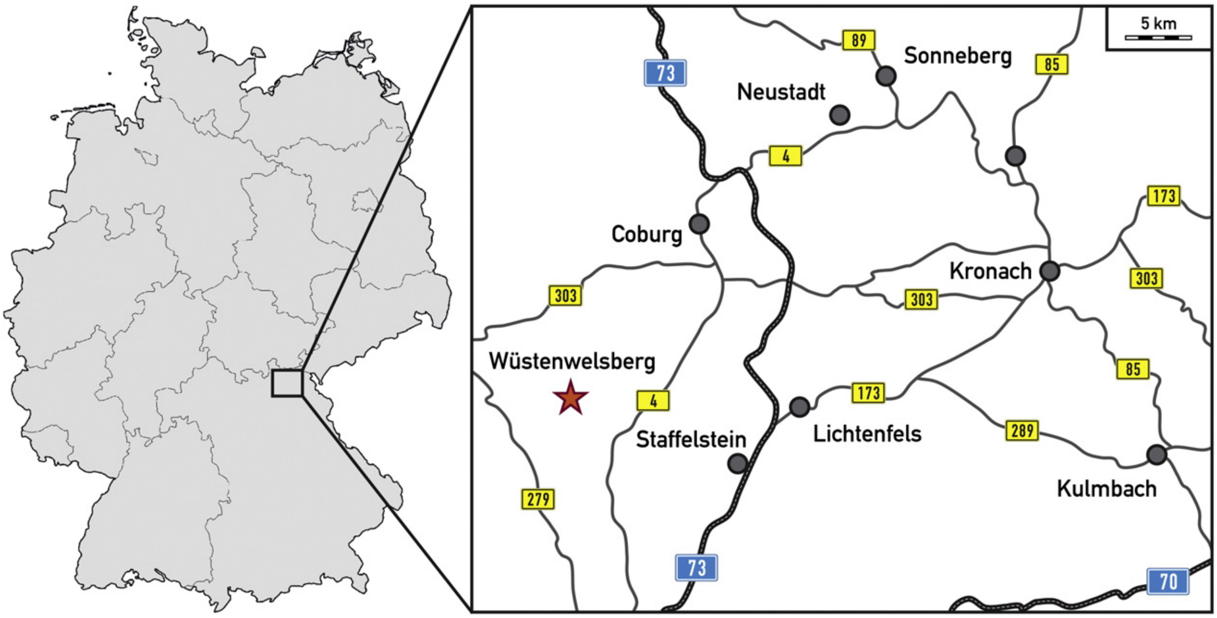

Fig. 1. Map of Germany indicating the position of the locality of Wüstenwelsberg in Franconia (red star).

2. Material and methods

2.1. The Wüstenwelsberg quarry

The studied section is located in a sandstone quarry near the village of Wüstenwelsberg, approximately 20 km SW of Coburg, Germany (Fig. 1). The sedimentary rocks were deposited in the Germanic Basin, and are characterised by an alternation of claystone and sandstone layers (for details see Bonis et al., 2010). The plant fossils derive from the claystones, one of which is the so-called 'Hauptton' that can be up to 10 m thick. Most of the fossil bennettitalean specimens originate from this bed (level 3 in Bonis et al., 2010), but level 2 (just below the 'Hauptton') also contains some remains. *Pterophyllum aequale* is especially common there; in many cases, it covers whole slabs and is commonly associated at this level with *Bennettistemon bursigerum*, which is the potential microsporophyll of the plant producing this foliage. The bed hosting *P. aequale* and *B. bursigerum* is slightly more grayish with less clay and a slightly more sand than the rest of the 'Hauptton'. No bennettitaleans were found in level 1 of Bonis et al. (2010).

2.2. Description of the fossil material

The fossil leaf material used in this study was collected during fieldtrips by the authors. The fossils are stored in the collections of the Laboratory of Palaeobotany and Palynology, University of Utrecht, The Netherlands (UU numbers), and in the private collections of Stefan Schmeissner, Kulmbach, Germany (numbers preceded by Q) and Günter Dütsch, Untersteinach, Germany (numbers containing the acronym wü). The fossil plant remains are mainly compression fossils of a relatively small size, but cuticle remains could easily be prepared and so added to our knowledge of the bennettitaleans in this Rhaetian flora. Cuticle samples were processed from several specimens and this proved essential for unambiguous species identification. Those specimens are marked with the suffix (c) in the 'Material examined' lists.

2.3. Methods

Cuticles were picked directly from the rock surface. They were macerated according to the standard procedure (e.g., Kerp, 1990; Pott and Kerp, 2008; Pott and McLoughlin, 2009) using Schulze's reagent (30% HNO_3 with a few $KClO_3$ crystals) and were subsequently treated with 5%–10% ammonia (NH_4OH) or potassium hydroxide (KOH). The 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 Stefan Schmeissner and Günter Dütsch. Those slides and specimens will be donated to a publicly available collection after the research on the Wüstenwelsberg flora has been completed.

The macrofossil specimens were photographed with a Nikon D80/Nikkor AF-S Mikro 60-mm 1:2.8G ED system digital camera. Oblique lighting and polarizing filters in front of both the camera lenses and the lights were used to enhance contrast and fine details. The cuticles were analysed with an Olympus BX-51 light microscope, which was modified for epifluorescence microscopy, and photographed with an Olympus DP-71 digital camera.

3. Description of species

Order Bennettitales Engler, 1892
Family Williamsoniaceae Carruthers, 1870

Genus *Pterophyllum* Brongniart, 1825

Diagnosis and discussion: See Harris (1932b, 1969); Pott et al. (2007b, 2007c) and Pott and McLoughlin (2009).

Type species: *Pterophyllum filicoides* (Schlotheim, 1822) Zeiller, 1906, from the Carnian (Upper Triassic) of Neuewelt, Basel, Switzerland (see Pott et al., 2007c).

Pterophyllum aequale (Brongniart, 1825) Nathorst, 1878, emend. Pott and McLoughlin, 2009.
Plate I, 1, 2, Plate V, 1, 2.

Synonymy and references:
1825 *Nilssonia*? *aequalis* — Brongniart, p. 219; pl. 12, fig. 6.
1833 *Zamites aequalis* Presl — Sternberg, p. 198; no illustration.
1878 *Pterophyllum aequale* Brongniart — Nathorst, p. 18–19; pl. 2, fig. 13; p. 48–49; pl. 6, figs 8–11.
2009 *Pterophyllum aequale* (Brongniart) Nathorst — Pott and McLoughlin *cum syn.*, p. 125; pl. 2, figs 1–12; pl. 3, figs 1–8; text-fig. 4.

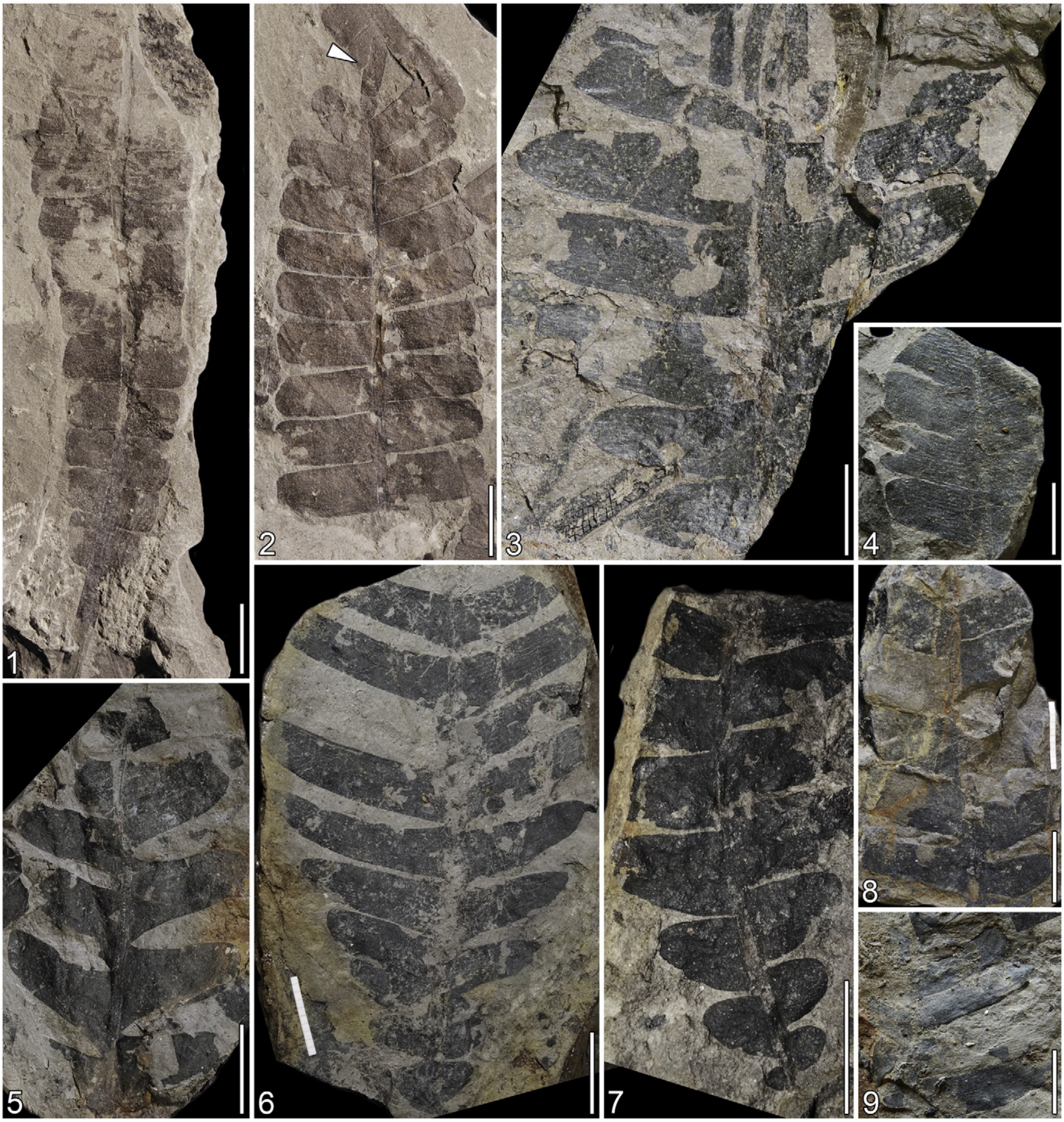

Plate I. Leaves of *Pterophyllum aequale*, *P. astartense* and *P. kochii* from the Rhaetian of Wüstenwelsberg. 1. *P. aequale*, 111wü09. 2. *P. aequale*, 116wü09. 3. *P. astartense*, Q245/02. 4. *P. astartense*, Q431/06. 5. *P. astartense*, Q974/02. 6. *P. astartense*, Q359/03. 7. *P. astartense*, Q966/14. 8. *P. kochii*, Q883/11. 9. *P. kochii*, 03wü03. Scale bars—10 mm.

2011 *Pterophyllum aequale* (Brongniart) Nathorst — Pott and McLoughlin, p. 1038; text-figs 8A–D, 9C.

Description: The specimens found at Wüstenwelsberg conform exactly to the description of the material from Jameson Land and Scania that is provided by Harris (1932b; as *Pterophyllum schenkii*) and Pott and McLoughlin (2009), and there is no doubt that they are conspecific. The leaves show the same outline and shape of the whole lamina and the individual leaflets, the same arrangement and insertion of the leaflets, the characteristic depression on the leaflet apices, equivalent venation patterns and identical central depression and transverse wrinkles on the centre of the upper side of the rachis (Plate I, 1, 2). Even the texture and preservation of many of the fossils are identical. The cuticle fragments isolated from the Wüstenwelsberg specimens are identical to those of the specimens from Scania and Jameson Land and have the same arrangement and architecture of the stomata on the abaxial side of the leaves and the diagnostic small central solid papilla on the epidermal cells of both surfaces. The cell walls are straight as in the specimens from Scania and Jameson Land (Plate V, 1, 2).

The foliage from Wüstenwelsberg provides more information on the shape of the whole leaves than previously known because basal and apical portions are preserved in some specimens. Basal-most leaflets continuously decrease in length and become more rectangular or quadrate, before the lamina runs out into a naked petiole. Apically, the last two to three pairs of leaflets are shorter than those in the central portion, forming a bluntly rounded apex. An apical leaflet is preserved in one specimen (Plate I, 2), which is more slender than the other leaflets and slightly shorter than the lateral leaflets. It lacks the characteristic central depression, but has a more acute apex (cf. Harris, 1932b, text-fig. 23A).

Measurements: The longest portion of a leaf found at Wüstenwelsberg is 170 mm long (incomplete leaf); leaves are up to ca. 40 mm wide at their widest portion. The individual leaflets reach up to 18 mm long and 8 mm wide. The rachis measures 4 mm wide in its proximal portion and retains its width almost until the apex. The petiole is up to 26 mm long and the apical leaflet reaches 8 mm in length.

Remarks: The leaves found at Wüstenwelsberg are considered conspecific with those described as *Pterophyllum aequale* from Jameson Land and Scania by Harris (1932b; as *P. schenkii*) and Pott and McLoughlin (2009) based on exact agreement in all macro- and micromorphological features available. The leaves from Wüstenwelsberg expand our knowledge of the shape and outline of the foliage as they provide basal and apical portions or even completely preserved leaves that were not known from Jameson Land or Scania (see Harris, 1932b; Pott and McLoughlin, 2009). *Pterophyllum aequale* is, as is the case in Jameson Land and Scania, widely represented in Wüstenwelsberg and constitutes one of the dominant plant species within the assemblage. It is especially common in a specific part of level 2, that is, level 2A. Here it covers whole slabs and is commonly associated not only with *Welsbergia bursigera* (see later), but also with the peltasperm seedfern *Lepidopteris ottonis*. Other plant fossils are very rare at this level (sparse occurrences of the ferns *Phlebopteris* and *Dictyophyllum* and the conifer *Stachyotaxus*). Moreover, the species is also widely distributed in other Rhaetian assemblages of the Northern Hemisphere, such as Bornholm, Ukraine (Donets Basin) and Iran (Alborz) (Möller, 1902, 1903; Zeiller, 1903; Stanislavski, 1971; Schweitzer and Kirchner, 2003; Pott and McLoughlin, 2009). Hence, this species has a broad geographic distribution, although significantly, all occurrences were located at ca. 30° N palaeolatitude (see Pott and McLoughlin, 2009).

Material examined: Q140/02, 294/03(c), 418/05(c), 454/06–459/06, 564/08(c), 593/08(c), 594/08, 643/08, 659/08, 676/08, 680/08, 720/08, 744/09, 745/09, 746/09, 749/09–751/09, 756/09, 757/09, 764/09–766/09, 769/09(c), 771/09–773/09, 775/09, 779/09, 794/09–798/09, 799/09(c), 800/09, 812/09, 813/09, 819/10–823/10, 830/10, 832/10, 834/10–837/10, 840/10, 841/10, 844/10–846/10, 850/10, 863/11, 876/11, 889/11, 896/12, 952/14, 969/14, 985/15, 987/15, 990/15–992/15; 79wü03, 20wü08, 01wü09, 13wü09, 18wü09, 20wü09, 23wü09–31wü09, 33wü09–36wü09, 40wü09, 44wü09, 47wü09, 49wü09–56wü09, 60wü09, 62wü09, 64wü09–72wü09, 78wü09–80wü09, 82wü09, 93wü09, 94wü09, 96wü09, 100wü09, 104wü09, 111wü09–119wü09, 04wü14, 06wü14, 12wü14, 13wü14, 16wü14.

Pterophyllum astartense Harris, 1932b.
Plate I, 3–7, Plate V, 3–6.

Synonymy and references:
1932b *Pterophyllum astartense* — Harris, p. 44; pl. 4, fig. 10; text-figs 19–21.
1937 *Pterophyllum astartense* Harris — Harris, p. 50; no illustration.
1990 *Pterophyllum astartense* Harris — Wang and Chen, p. 727; pl. 1, figs 7, 8; pl. 22, figs 14–19.
non 2007 *Pterophyllum astartense* Harris — Vavrek et al., p. 1655; text-fig. 3C.

Description: Leaves assigned to *Pterophyllum astartense* are inverse-ovate or obovate to oblong in gross outline, regularly segmented into leaflets that are inserted by the full width of their base laterally on the prominent rachis. The rachis bears characteristic transverse wrinkles basally; it decreases continuously in width from the broad, naked petiole until almost evanescing apically. Leaflets are inserted oppositely to sub-oppositely at angles of 75°–85°; the leaflets are falcate to slightly arcuate with a concave adaxial margin and a convex abaxial margin, retaining their width or tapering only slightly until the last fourth of their length, where both margins more abruptly taper to a bluntly rounded apex. More distal leaflets have apices that are more acutely rounded with the pointed tip shifted towards the adaxial margin. The leaflets are basally expanded (decurrent) basiscopically; the more proximal leaflets also are acroscopically expanded. The most proximal leaflets are very short and thus appear roundish; they usually overlap imbricately whereas more distal ones (those inserted in the distal 2/3 of the leaf) do not overlap; the gaps between the leaflets increase in width toward the leaf apex. The most distal two pairs of leaflets are more arcuate than the remaining ones and are bent crescent-like to falcate towards the apical leaflet. The latter is ovate in outline but of much smaller size than the lateral leaflets. The venation of the leaflets is prominent; the parallel veins enter at almost right angles from the rachis, bifurcate once close to the base of the leaflet and proceed straight to the margin always keeping their distance; some of the veins bifurcate sporadically (Plate I, 3–7).

The diagnostic cuticles reflect an epidermis that conforms to the detailed description of Harris (1932b). The leaves are hypostomatic and produce robust cuticles; adaxial and abaxial cuticles are equally thick; costal and intercostal fields are difficult to distinguish on the adaxial side, but are readily distinguishable on the abaxial side of the leaf. The stomata are restricted to the intercostal fields. In the adaxial epidermis, the cells of the intercostal areas are mostly elongate, rectangular to isodiametric. The epidermal cells positioned above the veins are longer and more slender. The anticlinal cell walls are straight and the periclinal cell walls are smooth. The costal fields in the abaxial epidermis are composed of narrowly rectangular epidermal cells. The anticlinal cell walls are sinuous, the periclinal walls are smooth. The intercostal fields consist of predominantly isodiametric, rectangular to quadrate epidermal cells with slightly to moderately sinuous anticlinal walls. The stomata are regularly scattered, brachyparacytic and orientated arbitrarily; the epidermal cells between stomata appear to be arbitrarily oriented as well. The diacytic stomata possess two rectangular subsidiary cells, slightly overhanging the pit mouth to form a slightly sunken stoma. Loosely, but regularly, scattered cells are present on the abaxial cuticle that each produce a hollow papilla (Plate V, 3–6).

Measurements: The leaf fragments found at Wüstenwelsberg are up to 100 mm long and up to 66 mm wide. The individual leaflets reach up to 31 mm long and 10 mm wide. The rachis is up to 2.9 mm wide in its proximal portion. The apical leaflet reaches 9 mm long.

Remarks: The leaves are regarded conspecific with those reported by Harris (1932b) from Jameson Land as *Pterophyllum astartense*. The leaves agree in all macro- and micromorphological characteristics that are available, not only in the shape of laminae and leaflets, but also in the dimensions and epidermal details including the characteristic papillae on the lower leaflet surface and the transverse wrinkles on the upper side of the rachis. The Jameson Land specimens contain a few leaves that are larger than those in the German material, with longer pinna (up to 55 mm long), but the majority of the Jameson Land leaves are equal in size to those from Wüstenwelsberg. Moreover, for the Jameson Land specimens, a slightly higher vein density is reported, but this can be surveyed in only one figured specimen. *Pterophyllum astartense* was apparently endemic to the Rhaetian of Jameson Land; it has not been reported from any of the classic Rhaetian localities that share numerous taxa with the Rhaetian of Jameson Land, such as Scania, the Donets Basin, Alborz or Tonkin (Zeiller, 1903; Stanislavski, 1971; Kelber and Van Konijnenburg-van Cittert, 1997; Schweitzer and Kirchner, 2003; Pott and McLoughlin, 2009). The only record outside Greenland was reported by Vavrek et al. (2007), who found *P. astartense* in the Rhaetian of

Ellesmere Island, Arctic Canada. However, the description of those specimens and the only one illustrated differ greatly from those reported by Harris (1932b) and those from Wüstenwelsberg; no epidermal anatomy is available from the Canadian specimens and to us, they are not at all conspecific. We, therefore, reject the identification of these specimens as *P. astartense*. The specimens from Wüstenwelsberg are, consequently, the only ones found beyond Greenland so far.

Whether those specimens reported by Pott and McLoughlin (2009) as *Pterophyllum irregulare* Nathorst from the Rhaetian of Scania are conspecific with *P. astartense* is difficult to ascertain as the material from Scania is very fragmentary and poorly preserved, but it is likely that those specimens constitute the same species. Pott and McLoughlin (2009) refrained from assigning the Scanian specimens to *P. astartense* due to slight differences in leaflet width and anticlinal cell wall nature, which is, based on the small sample size, a weak argument. However, we also refrain here from regarding these species conspecific for the same reason and await further material for taxonomic clarification. Kelber and Van Konijnenburg-van Cittert (1997) reported *Pterophyllum* sp. from the Rhaetian of Heilgersdorf, Bavaria. Their specimen is superficially similar to *P. astartense*, but a more resolved taxonomic assignment could not be made due to the lack of preserved cuticle.

Material examined: Q91/02–93/02(c), 96/02, 97/02, 98/02(c), 99/02, 100/02, 103/02, 106/02–109/02, 122/02, 123/02, 127/02, 135/02, 136/02, 149/02, 150/02(c), 168/02(c), 170/02, 171/02, 174/02–176/02, 185/02(c), 190/02, 192/02, 193/02, 195/02, 200/02(c), 201/02(c), 202/02(c), 207/02(c), 208/02, 231/02, 232/02, 245/02, 251/02, 256/03(c), 257/03(c), 261/03, 273/02, 276/02, 290/03, 291/03, 294/03, 300/03(c), 306/03(c), 311/03, 320/03(c), 325/03, 337/03, 356/03, 359/03(c)–361/03(c), 374/04, 395/04, 398/04, 420/05, 423/05, 430/06–438/06, 443/06, 447/06, 630/08, 633/08, 727/09, 869/11, 895/12, 898/12, 907/13–913/13, 925/13–927/13, 955/14, 959/14, 966/14, 974/14; 02wü02, 15wü02, 50wü02, 83wü02, 92wü02, 94wü02, 101wü02, 141wü02, 177wü02, 181wü02, 05wü03, 06wü03, 16wü03, 30wü03, 35wü03, 36wü03, 39wü03, 43wü03, 44wü03, 57wü03, 59wü03, 60wü03, 62wü03, 74wü03, 85wü03, 93wü03–95wü03, 100wü03, 108wü03, 112wü03, 123wü03, 124wü03, 03wü04, 07wü04(c), 14wü04, 19wü04, 26wü04, 43wü04(c), 48wü04, 50wü04, 02wü05, 08wü05, 10wü05, 17wü05F, 77wü08, 89wü08, 128wü08, 130wü08, 194wü08, 03wü12, 05wü12, 11wü12, 13wü12, 14wü12, 16wü12, 17wü12–20wü12, 22wü12, 24wü12–27wü12, 29wü12, 05wü13, 14wü13, 15wü13, 17wü13, 01wü14, 03wü14, 05wü14, 07wü14, 09wü14, 11wü14, 17wü14; UU23315, 23316, 23323, 23327. The following specimens are kept unassigned as *Pterophyllum* sp. because sufficient information for assignment to a formal species is not available; however, they most likely belong to *P. astartense*: Q142/02, 155/02, 158/02, 272/02, 376/04, 419/05, 448/06, 872/11, 886/11; 85wü02.

Pterophyllum pinnatifidum Harris, 1932b.
Plate II, 1–7, Plate V, 7, 8.

Synonymy and references:
1896 *Ptilozamites* sp.? — Hartz, p. 235; pl. 15, figs 2, 4, 7; pl. 16, fig. 1.
1896 *Anomozamites* cf. *inconstans* — Hartz, p. 235; pl. 16, figs 6, 8, 9.
1926 *Pterophyllum* sp. D — Harris, p. 96; text-fig. 21.
1932b *Pterophyllum pinnatifidum* — Harris, p. 55; pl. 8, fig. 8; text-figs 26–28.
1937 *Pterophyllum pinnatifidum* Harris — Harris, p. 51; no illustration
non 2011 *Pterophyllum pinnatifidum* Harris — Moisan et al., p. 99; pl. 2, figs 4, 5; pl. 3, figs 1 –8; pl. 4, figs 1–8; pl. 5, figs 8–10; pl. 6, figs 1–4.

Description: The leaves of *Pterophyllum pinnatifidum* are characterised by falcate to slightly arcuate tapering leaflets that in more proximal portions and in slender leaves become triangular. The leaflets are sub-oppositely inserted by their whole basal width lateral to the rachis at angles between 60° and 80°. The distal-most leaflets are inserted at more acute angles of ca. 40°. The basiscopic margin is convex and the acroscopic margin concave; the leaflet apices are bluntly rounded with a slightly pointed tip directed towards the leaf apex. The leaflet bases are in contact with their neighbours and connected by a 1–2 mm wide laminar wing along the rachis. The venation is parallel and prominent in most specimens; the veins bifurcate when entering the lamina and some bifurcate sporadically again during their course through the lamina. The upper surface of the rachis is commonly smooth, but in some cases is characterised by slight transverse wrinkles (Plate II, 1–7).

The epidermal anatomy corresponds closely to the description provided by Harris (1932b). The walls of the rectangular and elongate cells over the veins and of the isodiametric epidermal cells between the veins are characterised by predominantly straight to, in some cases, faintly sinuous anticlinal cell walls. The stomata are confined to the lower surface and of the brachyparacytic type. They are randomly scattered in the intercostal fields and commonly oriented irregularly. Hair cells have not been observed (Plate V, 7, 8).

Measurements: The preserved portions of leaves are up to 64.5 mm long and 34.5 mm wide. The leaflets reach 19–20 mm in length and are 8–10 mm wide basally. The thin rachis retains its width along the whole preserved portion and is 2.0–2.5 mm wide.

Remarks: The specimens from Wüstenwelsberg are all incomplete, but correspond well to those reported by Harris (1932b) from Jameson Land. The specimens even agree in all the epidermal details provided by Harris (1932b). The laminar wing along the rachis and their straight anticlinal cell walls distinguish them from *Anomozamites hartzii*, some specimens of which appear superficially very similar in macroscopic outline. Those specimens are also similar to *A. triangularis* from the Rhaetian of Scania (Pott and McLoughlin, 2009), but the latter are distinguished by the more acute basiscopic angle, the more pointed leaflet apices, the basally diverging veins and the characteristic laminar wing along the rachis. We regard the identification of the specimens assigned to *Pterophyllum pinnatifidum* by Moisan et al. (2011) from Madygen questionable as they come from much older assemblages (i.e., Carnian) and we are even uncertain whether the Madygen plant was a bennettitalean or a cycad because the authors were not able to clearly prove the bennettitalean nature of the leaves. The authors reported trichome bases, which are not present in *P. pinnatifidum*, and mention differences in leaflet width and incision. Therefore, we reject that record from *P. pinnatifidum*.

Material examined: Q95/02(c), 172/02, 173/02, 255/03(c), 271/02(c), 446/06, 451/06(c), 452/06, 874/11, 954/14; UU23309.

Pterophyllum kochii Harris, 1926.
Plate I, 8, 9, Plate VI, 1, 2.

Synonymy and references:
1926 *Pterophyllum kochi* — Harris, p. 89; pl. 7, fig. 6; text-fig. 17A–E
1932b *Pterophyllum kochi* Harris — Harris, p. 58; text-fig. 29.
1937 *Pterophyllum kochi* Harris — Harris, p. 52; no illustration
non 1950 *Pterophyllum kochi* Harris — Lundblad, p. 61; pl. 12, fig. 4; pl.13, fig. 3; text-fig. 23A–E.

Description: A few specimens have been found that are assigned to *Pterophyllum kochii*. These specimens yield portions of leaves with segmented laminae, whose densely arranged leaflets are generally straight and parallel-sided, but slightly arcuate in the distal portion of the leaf, free up to the base and not decurrent, and each is terminated by an evenly rounded apex. The leaflets are inserted at almost right angles laterally to the upper side of the thin rachis leaving its middle portion free. The leaflets are equally broad in the preserved portions and arranged sub-oppositely. The venation is parallel; the veins bifurcate after entering the leaflet and then proceed straight to the leaflet apex; rare additional bifurcations seem to be present; vein density in the middle of the leaflets is about 20–24 veins per centimeter (Plate I, 8, 9).

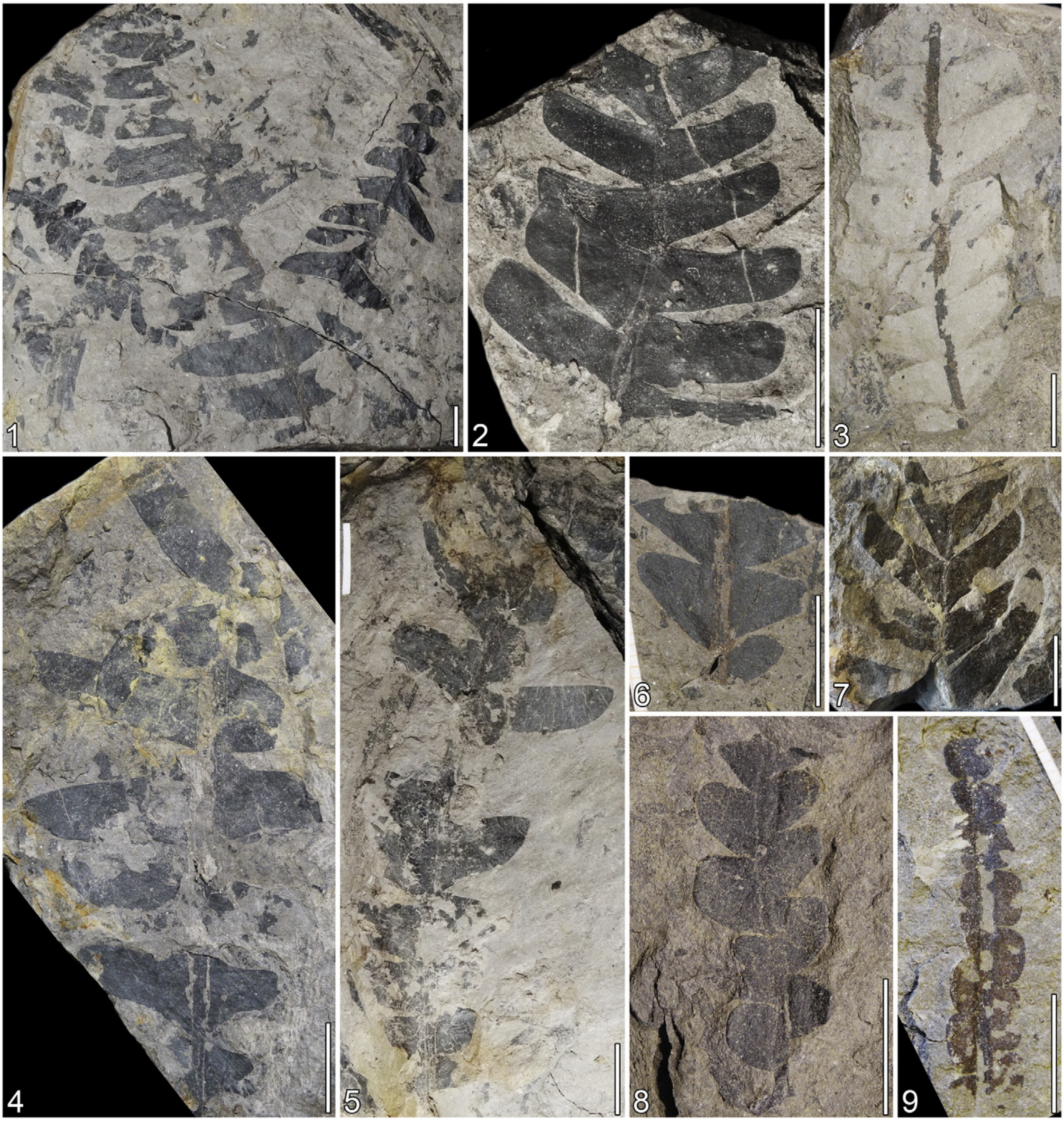

Plate II. Leaves of *Pterophyllum pinnatifidum* and *Anomozamites gracilis* from the Rhaetian of Wüstenwelsberg. 1. *P. pinnatifidum*, Q438/06. 2. *P. pinnatifidum*, Q954/14. 3. *P. pinnatifidum*, Q452/06. 4. *P. pinnatifidum*, Q874/11. 5. *P. pinnatifidum*, Q255/03. 6. *P. pinnatifidum*, Q451/06. 7. *P. pinnatifidum*, Q095/02. 8. *A. gracilis*, 08wü13. 9. *A. gracilis*, Q782/08. Scale bars — 10 mm.

The rectangular and elongate epidermal cells possess straight anticlinal cell walls at the margins of the leaflets and over the veins on the upper (adaxial) leaf surface, whereas the walls become strongly sinuous over the veins and in intercostal fields on the lower (abaxial) leaf surface. The epidermal cells in the latter are more isodiametric and irregularly arranged than elongate and arranged in rows as is the case in costal fields. The stomata are confined to the intercostal fields on the lower surface, brachyparacytic and oriented transversely. Hair cells or papillae occur on the lower surface, but are absent from the upper surface (Plate VI, 1, 2).

Measurements: The preserved portions of leaves are up to 62.5 mm long and 37.4 mm wide. The leaflets reach 32.5 mm in length and are basally 7–9 mm wide in the middle portion of the leaves. The 1.5–2 mm wide rachis maintains its width along the whole preserved portion.

Remarks: The leaves from Wüstenwelsberg correspond very well with the descriptions and illustrations provided by Harris (1932b) for leaves from Jameson Land, in both macro- and epidermal morphology, and there is no doubt that these leaves are conspecific. The name, however, is nowadays correctly spelled *Pterophyllum kochii* (McNeill et al., 2012, Art. 60.11). To our knowledge, *P. kochii* has so far been reported from Jameson Land only. The specimens assigned to this species by Lundblad (1950) from the Rhaetian of Scania were recently identified as *P. angustifolius* by Pott and McLoughlin (2009) and were thus reallocated to *Wielandiella angustifolia* (Pott, 2014a, 2014b). *Pterophyllum kochii* is common in Jameson Land (Harris, 1932b), whereas it constitutes only a minor component (six specimens) of the collections from Wüstenwelsberg.

Material examined: Q275/02(c), 883/11(c); 59wü02, 03wü03, 48wü04; UU23312.

Genus *Anomozamites* Schimper, 1870, emend. Pott et McLoughlin, 2009.

Diagnosis and discussion: See Pott and McLoughlin (2009).
Type species: *Anomozamites nilssonii* (Phillips, 1829) Harris, 1969, from the Bajocian (Middle Jurassic) of Cayton Bay, Yorkshire, U.K.

Anomozamites gracilis Nathorst, 1876, emend. Pott et McLoughlin, 2009.
Plate II, 8, 9, Plate VI, 3, 4.

Synonymy and references:
1876 *Anomozamites gracilis* — Nathorst, p. 43–45; pl. 12, figs 4–12.
2009 *Anomozamites gracilis* Nathorst — Pott and McLoughlin *cum syn.*, p. 142; pl. 9, figs 1–9; pl. 10, figs 1–9; text-fig. 4.

Description: A few specimens yield extremely small leaves that have the typically rectangular, apically rounded, short and broad leaflets of *Anomozamites gracilis*. The lamina is narrow and linear in outline, and regularly segmented in the preserved leaf portions. The leaflets are inserted by their full basal width laterally on the rachis at an angle of 80°–90° and are more or less parallel-sided; their apices being rounded give the whole leaflets an almost circular shape. The lamina is exposed and leaflets are inserted sub-oppositely to alternately in the preserved leaves from Wüstenwelsberg (Plate II, 8, 9).

The hypostomatic leaves have robust cuticles; the costal and intercostal fields are similar on the cuticles from both surfaces. The epidermal cells of the adaxial (upper) side are arranged in distinct rows, isodiametric (rectangular) in outline, with straight anticlinal walls at the polar ends, but broadly undulate on the lateral sides. The cuticular wedges extend deeply into the intercellular spaces between the epidermal cells. No papillae were found on the upper leaf surface. The stomata are confined to the abaxial epidermis in areas that can be interpreted as the intercostal fields. The polygonal and weakly rectangular epidermal cells are more or less arbitrarily arranged, that is, not in distinct rows as evident in the adaxial cuticle. All cell walls are widely undulate. The brachyparacytic stomata are regularly scattered on the epidermis, diacytic and orientated arbitrarily, but always orientated perpendicular to the cuticular opening, which is the outer 'stomatal chamber' (see Pott and McLoughlin, 2009). They are deeply sunken with two rectangular subsidiary cells creating a sunken stoma by overarching the pit mouth. The diagnostic subsidiaries are also sunken and each is completely superimposed by a normal epidermal cell. In some cases, the adjacent stomata are clustered and share the outer stomatal chamber seen as a small depression (or cuticular crypt) surrounded by a thick cuticular edge bearing overarching papillae (Plate VI, 3, 4).

Measurements: The preserved portions of leaves are up to 31 mm long and 6–10 mm wide. The leaflets reach 5.5–5.7 mm in length and are 5–6 mm wide basally. The 1.3–2.0 mm wide rachis maintains its width along the whole preserved portion.

Remarks: The specimens from Wüstenwelsberg conform exactly to the species description and illustrations provided by Pott and McLoughlin (2009) in measurements and characters, including detailed features of their epidermal anatomy. Pott and McLoughlin (2009) pointed out that *Anomozamites gracilis* is separated from *A. angustifolius* by the small leaf size and its rectangular, apically rounded, short and broad leaflets and by its almost isodiametric rather than markedly elongate cells, apparently denser undulation of anticlinal cell walls and by deeply sunken stomata including sunken subsidiary cells.

Material examined: Q767/09, Q782/09; 129wü02, 08wü13(c); UU23337, 23345A.

Genus *Nilssoniopteris* Nathorst, 1909a, emend. Pott et al., 2007a.

Diagnosis and discussion: See Cleal et al. (2006); Pott et al. (2007a) and Pott and Launis (2015).
Type species: *Nilssoniopteris tenuinervis* Nathorst, 1909a, from the Bajocian (Middle Jurassic) of Cloughton Wyke, Yorkshire, UK (see Cleal et al., 2006; Pott and Launis, 2015).

Remarks: We have identified numerous specimens assignable to *Nilssoniopteris*. During our examination, we realised that for a sound allocation to either nominal species (*N. jourdyi* or *N. ajorpokensis*), knowledge of the epidermal anatomy is essential as outlined already by Harris (1932b). Therefore, we have only allocated those specimens where information on epidermal anatomy is available and have assigned the remainder to *Nilssoniopteris* sp.

Nilssoniopteris jourdyi (Zeiller, 1886) Florin, 1933.
Plate III, 1, 2, 4, 5, 6.

Synonymy and references:
1886 *Macrotaeniopteris jourdyi* — Zeiller, p. 459; pl. 25, figs 1–3.
1903 *Taeniopteris jourdyi* — Zeiller, p. 66; pl. 10, figs 1–6; pl. 11, figs 1–4; pl. 12, figs 1–4, 6; pl. 13, figs 1–5.
1932b *Taeniozamites jourdyi* — Harris, p. 36; pl. 4, figs 2, 6, 8; text-fig. 14.
1933 *Nilssoniopteris jourdyi* (Zeiller) — Florin, p. 5; no illustration
?1934 cf. *Taeniopteris jourdyi* — Prynada, p. 21; pl. 2, fig. 2.
1937 *Nilssoniopteris jourdyi* (Zeiller) Florin — Harris, p. 50; no illustration.
1976 *Nilssoniopteris jourdyi* — Li et al., p. 124; pl. 36, figs 2, 3; pl. 37, figs 4–6.
1982a *Nilssoniopteris jourdyi* (Zeiller) Florin — Wu, p. 57; pl. 4, fig. 7A; pl. 8, fig. 5C.
1982b *Nilssoniopteris jourdyi* (Zeiller) Florin — Wu, p. 95; pl. 1, fig. 5B; pl. 4, fig. 4B; pl. 17, fig. 5A; pl. 19, fig. 5A.
1983 *Taeniopteris* cfr. *jourdyi* Zeiller — Kimura and Tsujii, p. 50; pl. 13, figs 9–10; pl. 14, fig. 6; text-fig. 12

Description: Two specimens (Q385/04, 404/04) can be allocated to *Nilssoniopteris jourdyi* unequivocally based on their epidermal anatomy. The specimens show the proximal portion of a leaf with an entire-margined lamina that is laterally inserted on a prominent rachis. The lamina tapers towards the basal end of the leaf, being asymmetrically terminated basally (i.e., on one side ending 2 mm more proximal than on the other side). The margin is slightly and irregularly wavy, which conforms to the specimens figured by Harris (1932b). The smooth rachis retains its width in the preserved portion; venation is not readily discernible, but appears parallel, with veins entering at right angles (Plate III, 1, 2).

The epidermal anatomy corresponds exactly to that described by Harris (1932b). The upper epidermis consists of rectangular cells with straight or slightly undulate anticlinal cell walls, with the cells along the veins narrower than those in the intercostal fields. Some form a small, faintly marked papilla in their central periclinal surface. On the abaxial side, the epidermal cells are rectangular with similarly straight to slightly sinuous anticlinal cell walls and a papilla at the centre of the periclinal surface. The stomata are confined to the intercostal fields, are almost all oriented transverse to the veins and of the brachyparacytic, diacytic type. Harris (1932b) called the subsidiary cells 'unspecialised' and, indeed, they are little different from normal epidermal cells (Plate VI, 5, 6).

Measurements: The leaves from Wüstenwelsberg are all fragmentary. The preserved portions of the two leaves are 13 mm and 48 mm

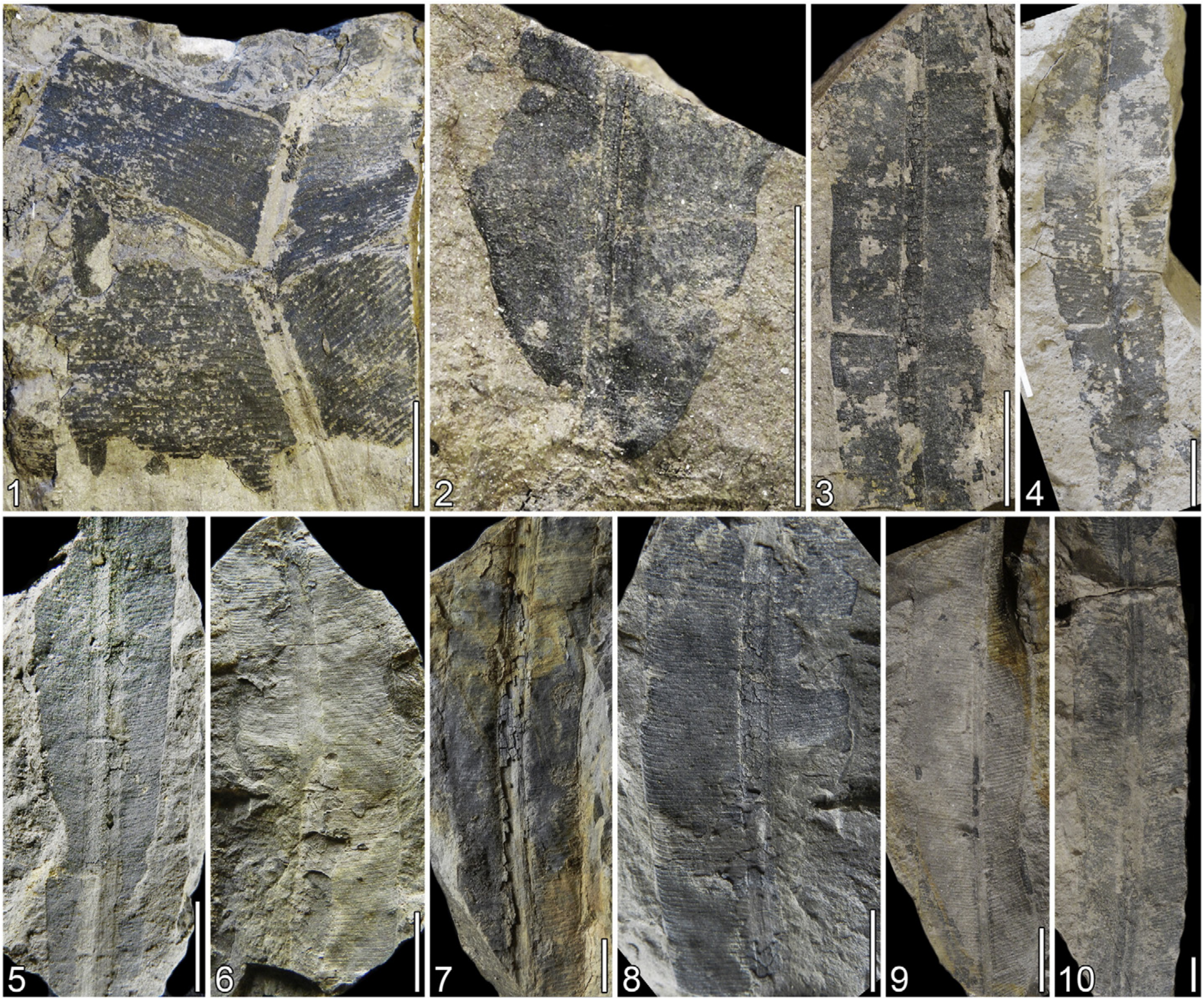

Plate III. Leaves of different *Nilssoniopteris* species from the Rhaetian of Wüstenwelsberg. 1. *N. jourdyi*, Q385/04. 2. *N. jourdyi*, Q404/04. 3. *N. ajorpokensis*, Q332/03. 4. *N. ajorpokensis*, Q405/04. 5. *N. ajorpokensis*, 115wü08. 6. *N. ajorpokensis*, 43wü08. 7. *N. ajorpokensis*, 118wü08. 8. *Nilssoniopteris* sp., 54wü08. 9. *Nilssoniopteris* sp., Q937/13. Scale bars—10 mm.

long, and 11 mm and 38 mm wide at their widest portion. The rachis is 1 mm and 3 mm wide in the respective specimens.

Remarks: The leaves are unequivocally assigned to *Nilssoniopteris jourdyi* based on their straight to only slightly sinuous anticlinal cell walls, in contrast to the strongly sinuous cell walls of *N. ajorpokensis* (see later). The venation is almost invisible, but Harris (1932b) stated that it is denser than in *N. ajorpokoensis*, even if 50 veins per centimeter appears quite a high number. The cuticle of one specimen (UU23318) matches the species described here, but it is only a small leaf fragment; hence its attribution to *Nilssoniopteris* cf. *N. jourdyi.* Amongst the unassigned specimens, there may be a few more attributable to *N. jourdyi*, but the species is comparatively rare in Wüstenwelsberg; the same is true for the Jameson Land assemblages. However, *N. jourdyi* was apparently more common and more extensively distributed in Rhaetian–Hettangian floras further to the east (Zeiller, 1886, 1903; Prynada, 1934; Wu, 1982a, 1982b; Kimura and Tsujii, 1983). A species with particularly close resemblance to *N. jourdyi* has been reported from Shaoqiao, Hunan Province, PR China, as *N. xuiana* by Zhou (1989). It is distinguished from *N. jourdyi* by its smooth midrib and the scattered trichomes on both cuticles (Zhou, 1989). This is notable as *N. jourdyi* has not been reported from the major floras between the localities of Jameson Land/Franconia in the west and the SE Asia/Chinese/Japanese floras in the east. For comparison with other species, see later.

Material examined: Q385/04(c), 404/04(c); possibly here: UU23318.

Nilssoniopteris ajorpokensis (Harris, 1932b) Florin, 1933.
Plate III, 3–7, Plate VI, 7, 8.

Synonymy and references:
1932b *Taeniozamites ajorpokensis* — Harris, p. 39; pl. 4, figs 4, 7, 9; text-fig. 15.
1933 *Nilssoniopteris ajorpokensis* (Harris) — Florin, p. 5; no illustration.
1937 *Nilssoniopteris ajorpokensis* (Harris) Florin — Harris, p. 50; no illustration.

Description: The leaves of *Nilssoniopteris ajorpokensis* are characterised by an entire-margined lamina that is inserted laterally on a very prominent rachis. The lamina margin is almost straight with very faint, irregular indentions. It tapers gradually from the upper middle portion of the leaf to the base. The apex is rather abruptly and bluntly rounded, and, according to Harris (1932b), the apex is characterised by a tiny spine that is an extension of the rachis. The latter is transversely wrinkled and retains its width during almost its entire course, only tapering apically. The venation is regular; the veins enter the lamina at angles of 80°–85° and proceed, after basal bifurcation, straight to the margin; sparse marginal bifurcations may occur. The vein density is about 10–13 per centimeter in the specimens from Wüstenwelsberg (Plate III, 3–7).

The epidermal anatomy is identical with that described and illustrated by Harris (1932b) from Jameson Land specimens. The most diagnostic character (when compared with *Nilssoniopteris jourdyi*) is the strongly sinuous anticlinal cell walls of the epidermal cells on both the ad- and abaxial surfaces, and the absence of any median papillae on the periclinal cell surfaces. The brachyparacytic stomata are diacytic, confined to intercostal fields in the abaxial epidermis and irregularly oriented. The subsidiary cells are small, more heavily cutinised than the surrounding epidermal cells and overarch the guard cells slightly and by this creating a weakly sunken stoma. Even the hollow papillae ('hair cells' of Harris, 1932b) are visible on some of the cuticles (Plate VI, 7, 8).

Measurements: The leaves from Wüstenwelsberg are all fragmentary. The longest preserved portions are up to 109.3 mm long and usually around 29.4–34.0 mm wide; some leaves, however, display a width of up to 58.9 mm in more distal leaf portions. The rachis may be widened in the (presumed) central portions of leaves up to 4.7 mm; in proximal and distal leaf portions, the rachis narrows down to usually 2.3–3.6 mm wide.

Remarks: The specimens conform well to those reported by Harris (1932b) from Jameson Land, not only in macromorphology and dimensions, but also in diagnostic details of the epidermal anatomy. Therefore, we regard the specimens from Wüstenwelsberg as conspecific. In Jameson Land, *Nilssoniopteris ajorpokensis* is abundant (dominant) in one bed (Harris, 1932b). From outside Greenland, the record from Wüstenwelsberg is the only one that we are aware of, which is in contrast to the wider distribution of *N. jourdyi*. There are several species from Rhaetian–Hettangian deposits that are comparable to both *N. ajorpokensis* and *N. jourdyi*, of which *N. zirabensis* from the Hettangian of Alborz is the most similar in terms of macromorphology and dimensions (Schweitzer and Kirchner, 2003). Its cuticle, however, cannot be compared in detail as the descriptions and illustrations by Schweitzer and Kirchner (2003) are insufficiently detailed. Zhou (1989, p. 144) described *N. oligotricha* from Shaoqiao in Hunan Province, PR China, which he compared with *N. ajorpokensis*, as "no doubt one of the most like species". *Nilssoniopteris oligotricha* is distinguished from *N. ajorpokensis* by its wrinkled midrib, the heavily cutinised subsidiary cells and the shape and length of the petiole (Zhou, 1989). So far, no *Nilssoniopteris* species has been described from the Rhaetian of Scania (Pott and McLoughlin, 2009, 2011); those assigned to the genus by Lundblad (1950) have been re-identified as species of *Anomozamites* by Pott and McLoughlin (2009).

Schweitzer and Kirchner (2003) described several additional *Nilssoniopteris* species from the Rhaetian–Hettangian of Iran and Afghanistan, including *N. musaefolia*, *N. schenkiana*, *N. intermedia* and *N. mikailovii*, all of which can easily be distinguished from *N. jourdyi* and *N. ajorpokensis* based on macro- and micromorphological characters (Sadovnikov, 1989; Schweitzer and Kirchner, 2003). The same is the case for Hettangian species from localities further to the east (e.g., Saint Petersburg, Transcaspian Oblast) that include, amongst others, *N. latifolium*, *N. linearis* and *N. papillifera* (Kiritchkova and Kalugin, 1973; Myatluk et al., 1973; Vakhrameev, 1991).

Material examined: Q255/03(c), 332/03, 333/03(c), 349/03, 405/04(c), 542/08, 565/08(c), 572/08(c), 581/08(c), 17wü02, 07wü03, 115wü03, 43wü08, 54wü08, 115wü08, 118–126wü08, 136wü08, 01wü13, 02wü13, 04wü13, 06wü13. The following specimens are kept unassigned in *Nilssoniopteris* sp. (Plate III, 8–10) because information on epidermal anatomy for confident identification is not available; they most likely belong to *N. ajorpokensis*: Q584/08, 585/08, 587/08, 588/08, 597/08, 619/08, 622/08, 671/08(c), 681/08, 685/08, 731/09, 739/09, 740/09, 762/09, 763/09, 829/10, 856/11, 864/11, 870/11, 878/10, 904/12, 935/13–938/13, 967/14; 25wü04, 27wü04, 19wü09, 95wü09, 101wü09, 103wü09, 18wü13.

Genus *Wielandiella* Nathorst, 1910 [erratum slip on Nathorst, 1909b], emend. Pott, 2014a.

Diagnosis and discussion: See Pott (2014a).
Type species: *Wielandiella angustifolia* (Nathorst, 1880) Nathorst, 1913, from the Rhaetian (Upper Triassic) of Bjuv, Scania, Sweden (see Pott, 2014a).

Wielandiella angustifolia (Nathorst, 1880) Nathorst, 1913, emend. Pott, 2014a.
Plate IV, 1–7, Plate VII, 1–5.

Synonymy and references:
1880 *Williamsonia angustifolia* — Nathorst, p. 50; pl. 8, figs 8–10
1909b *Wielandia angustifolia* — Nathorst, *nom. illeg.*, p. 22; pl. 5, figs 1–14; pl. 6, figs 1–11.
1913 *Wielandiella angustifolia* (Nathorst) — Nathorst, p. 365; no illustration.
2009 *Anomozamites angustifolius* — Pott and McLoughlin, *cum syn.*, p. 145; pl. 11, figs 1–9; pl. 12, figs 1–14; pl. 13, figs 1–7; pl. 14, figs 1–10; text fig. 4.
2014 *Wielandiella angustifolia* (Nathorst) Nathorst — Pott, *cum syn.*, p. 471; text-figs 3–16, 18–20.
2014 *Wielandiella angustifolia* — Pott and McLoughlin, p. 307; text-figs 1, 2.

Description: The sterile leaves are small, slender and regularly paripinnate; the segmentation is more pronounced in the median and apical portions of the leaves, the proximal part is usually entire-margined. The leaves possess a short petiole, and are narrow and linear to lanceolate; the lamina is tapered slightly towards the apex and petiole. The leaflets are oppositely to sub-oppositely positioned, densely arranged and free up to the rachis; they are inserted by their whole basal width laterally to the rachis at angles of 70°–80° and are more or less falcate with the acroscopic margin slightly concave and the basiscopic strongly convex. The leaflet apices are rounded and the bases are usually not expanded; short leaflets are quadrate with rounded apices. The slender rachis has transverse wrinkles in some cases. Up to 15 parallel veins enter each leaflet and run straight to the apex; the veins usually fork no more than once in the basal part of the leaflet (Plate IV, 1–4).

The hypostomatic leaves show distinct costal and intercostal fields on the abaxial, but indistinct examples on the adaxial side of the leaf. The epidermal cells on the adaxial surface are generally elongate and rectangular, with broadly undulate anticlinal walls. Stomata are absent. The costal fields on the abaxial epidermis are composed of 3–4 cell rows with the individual cells elongate and roughly rectangular; they possess delicate and broadly undulate anticlinal walls. The individual epidermal cells in the intercostal fields are usually polygonal and isodiametric to slightly rectangular. The anticlinal walls are widely undulate. The stomata are regularly distributed within the intercostal fields, brachyparacytic, with the stomatal pores orientated arbitrarily. The two rectangular subsidiary cells create, by overarching the pit mouth, a slightly sunken stoma. Hollow papillae are scattered regularly on the abaxial side of the leaf (Plate VII, 1–3).

One specimen (132wü02; Plate IV, 7) yields the compression of an ovulate organ, 34.7 mm long and 21.3 mm wide, whereof only the outer layer of bracts is preserved. These bracts are narrow, up to 2.8 mm wide, lanceolate and arranged in a whorl originating at the presumed petiole of the ovulate cone, and encompassing the gynoecium completely; their acutely rounded apices probably touched above the top of the gynoecium. The bracts are characterised by strong transverse wrinkles (well defined in isolated specimens) and slight longitudinal striae. The very fine hairs or trichomes reported by Pott (2014a) from the adaxial surface are not evident in any of the macrofossils, but in the cuticle, the typical hair bases with their base cell and the two appendices

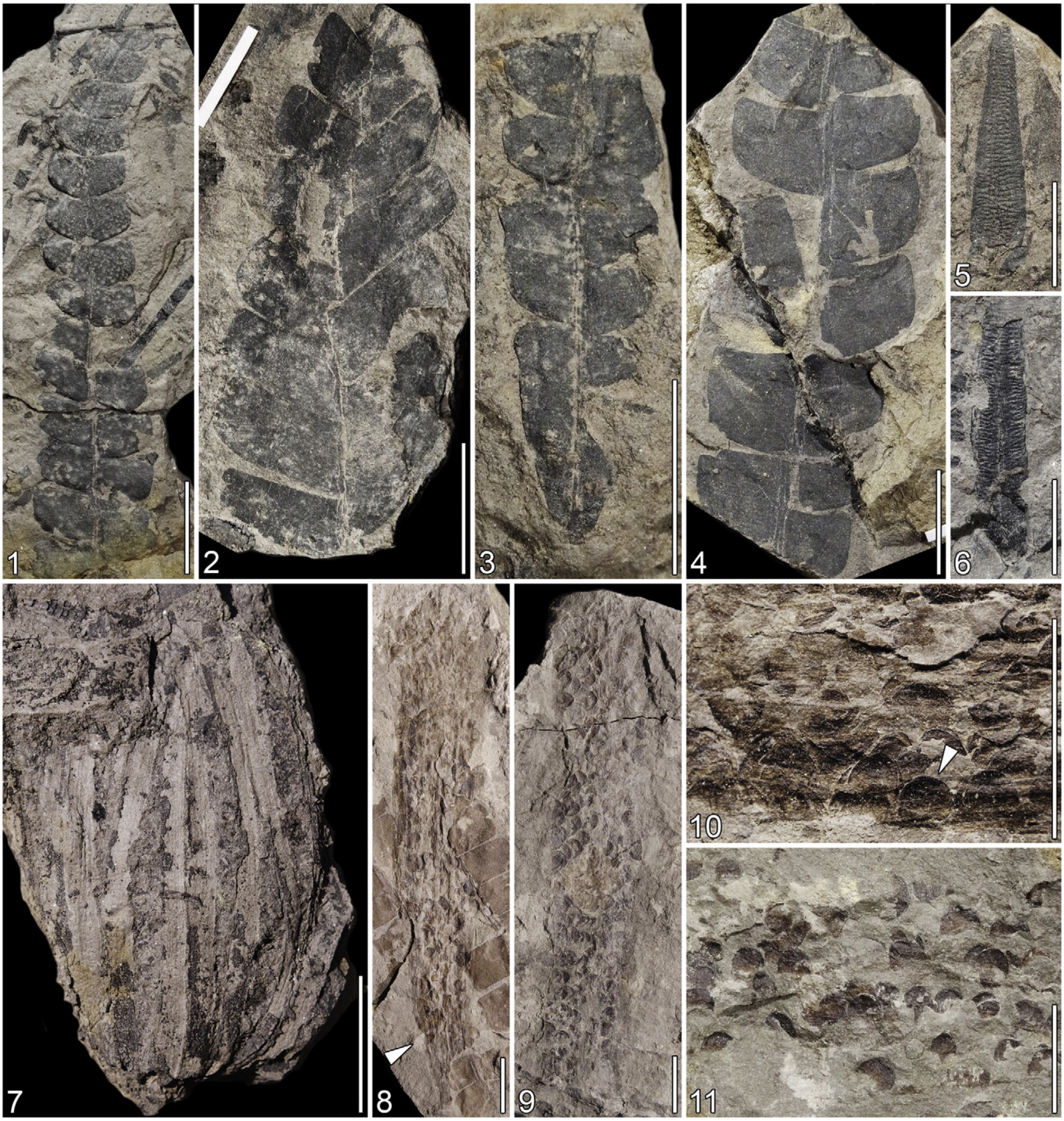

Plate IV. Sterile leaves, bracts and cone of *Wielandiella angustifolia*, and microsporophylls of *Welsbergia bursigera* from the Rhaetian of Wüstenwelsberg. 1. *Wielandiella angustifolia*, leaf, Q411/05. 2. *Wielandiella angustifolia*, leaf, Q754/09. 3. *Wielandiella angustifolia*, leaf, Q407/04. 4. *Wielandiella angustifolia*, leaf, Q690/08. 5. *Wielandiella angustifolia*, bract, Q330/03. 6. *Wielandiella angustifolia*, bract, Q638/08. 7. *Wielandiella angustifolia*, ovulate cone, 132wü02. 8. *Welsbergia bursigera*, 28wü09. 9. *Welsbergia bursigera*, 75wü09. 10. *Welsbergia bursigera*, 28wü09. 11. *Welsbergia bursigera*, 75wü09. Scale bars—10 mm.

could be observed (Plate VII, 4, 5). A few additional rock specimens yielded detached bracts (Plate IV, 5, 6). The bracts are also hyperstomatic; the costal and the intercostal fields are indistinct on both sides of the leaf. The abaxial epidermal cells are typically elongate, rectangular and regularly arranged in longitudinal rows. The anticlinal walls are straight; the stomata are absent on the abaxial side. The adaxial epidermis has a similar arrangement of the epidermal cells in longitudinal rows with straight anticlinal walls. Stomata and trichomes (hair bases) occur regularly distributed between the epidermal cells. The diacytic stomata are oriented perpendicular to the leaf margin and are brachyparacytic; the two rectangular subsidiaries create a slightly sunken stoma. The trichomes are of the same architecture as reported by Pott (2014a) and

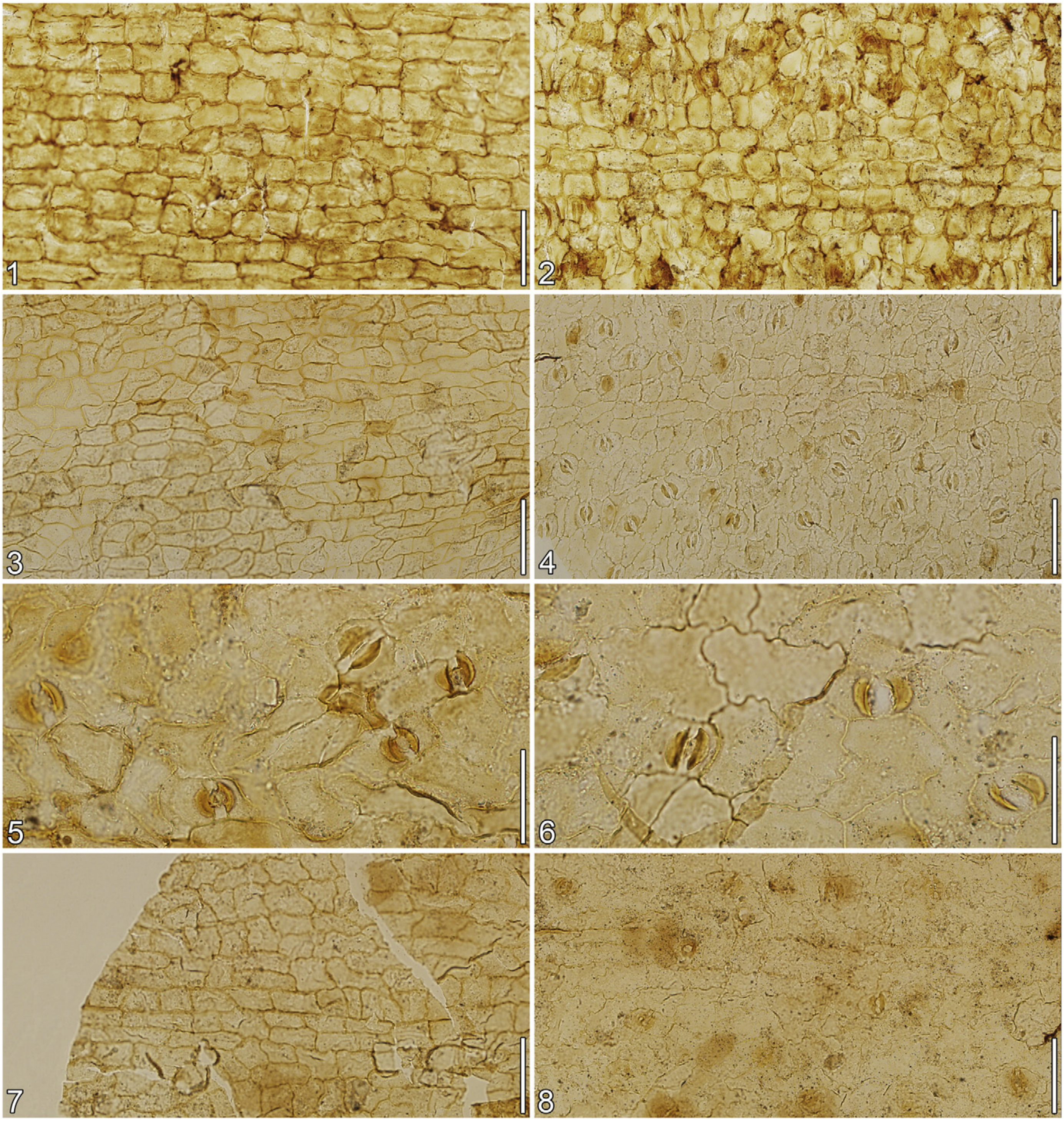

Plate V. Cuticles of different *Pterophyllum* species from the Rhaetian of Wüstenwelsberg. 1. *P. aequale*, adaxial cuticle, Nr398, 100 μm. 2. *P. aequale*, abaxial cuticle, Nr398, 100 μm. 3. *P. astartense*, adaxial cuticle, Nr355, 100 μm. 4. *P. astartense*, abaxial cuticle, Nr482, 100 μm. 5. *P. astartense*, adaxial cuticle, Nr355, 50 μm. 6. *P. astartense*, abaxial cuticle, Nr355, 50 μm. 7. *P. pinnatifidum*, adaxial cuticle, Nr497, 100 μm. 8. *P. pinnatifidum*, abaxial cuticle, Nr497, 100 μm.

typically cover two rows of epidermal cells in width; their base is circular and produces one or, more commonly, two hollow papillae or hairs that rise above the epidermis level (Plate VII, 4, 5).

Measurements: The preserved portions of sterile foliage are up to 89.4 mm long and 18.7 mm wide (two aberrant leaves had a leaf width up to 21.3 mm). The leaflets reach 8.8 mm in length but commonly are around 5.6–7.2 mm long; width of leaflets varies, but is commonly around 6.4–8.8 mm; sporadically, the leaflets are up to 12.3 mm wide. The thin rachis is 1.1–1.8 mm wide, but can be up to 2.0 mm wide basally and narrows usually down to 0.6–0.9 mm in apical portions. The bracts are 23.2–27.8 mm long and proximally 5.2–5.9 mm wide.

Remarks: *Wielandiella angustifolia* is a whole-plant taxon recently restored by Pott (2014a) including branched axes with sterile foliage and ovulate organs. The foliage was earlier identified as *Anomozamites angustifolius* by Pott and McLoughlin (2009), but later included in *W. angustifolia* by Pott (2014a). In Wüstenwelsberg, only sterile leaves, one ovulate organ and detached bracts from

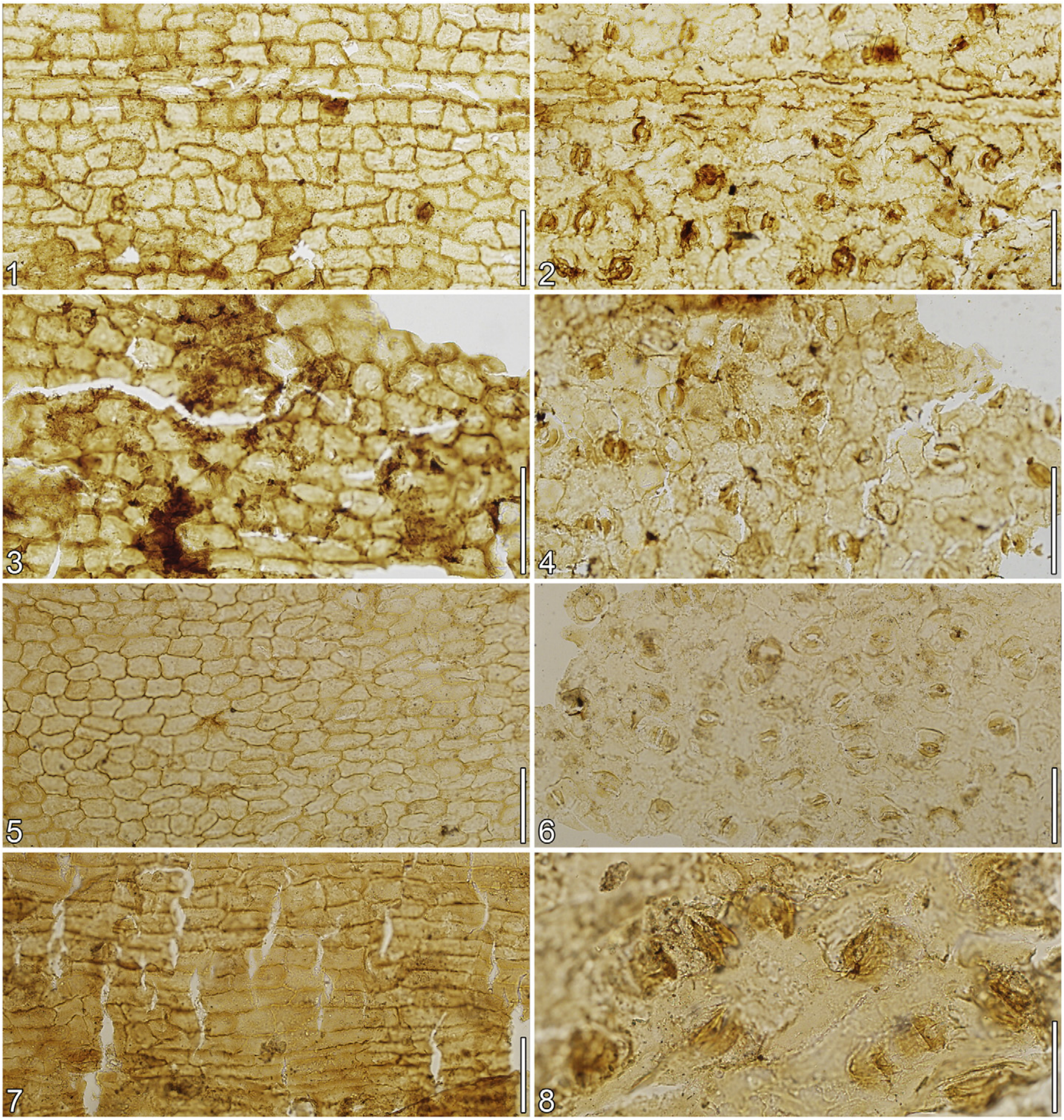

Plate VI. Cuticles of different *Pterophyllum*, *Anomozamites* and *Nilssoniopteris* species from the Rhaetian of Wüstenwelsberg. 1. *P. kochii*, adaxial cuticle, Q883/11-01, 100 μm. 2. *P. kochii*, abaxial cuticle, Q883/11-01, 100 μm. 3. *A. gracilis*, adaxial cuticle, 08wü13–02, 100 μm. 4. *A. gracilis*, abaxial cuticle, 08wü13–02, 100 μm. 5. *N. jourdyi*, adaxial cuticle, Q691/01-01, 100 μm. 6. *N. jourdyi*, abaxial cuticle, Q691/01-01, 100 μm. 7. *N. ajorpokensis*, adaxial cuticle, Q581/08-02, 100 μm. 8 *N. ajorpokensis*, abaxial cuticle, Q581/08–02, 50 μm.

ovulate cones have been found so far, but they can be identified unequivocally as *W. angustifolia* based on the detailed descriptions and illustrations of their macromorphology and epidermal anatomy provided by Pott and McLoughlin (2009) and Pott (2014a). The fossils correspond exactly to those from Jameson Land and Scania, and have been discussed in detail by Harris (1932b), Pott and McLoughlin (2009), Popa (2014) and Pott (2014a). Because the latter two publications provide detailed comparisons and discussions, we refrain from further evaluation of this species.

Material examined: *Leaves*: Q100/02(c), 140/2(c), 141/02(c), 147/02, 178/02(c), 221/02(c), 236/02(c)–239/02(c), 246/02, 249/02, 259/03(c), 266/03(c), 285/03, 286/03, 289/03, 298/03(c), 299/03(c), 308/03, 310/03, 312/03, 338/03, 348/03, 369/04, 370/04, 380/04,381/04, 386/04,399/04, 407/04, 408/04(c), 410/05, 411/05, 466/06, 467/06, 543/08(c), 552/08, 553/08, 610/08, 624/08, 630/08, 631/08, 642/08, 644/08–647/08, 652/08, 677/08(c), 690/08, 691/08, 695/08, 696/08, 703/08, 704/08, 717/08, 721/08, 726/09, 754/09(c), 776/09, 777/09, 824/10–826/10, 865/11, 868/11, 873/11, 882/11, 885/11, 899/12, 906/12,

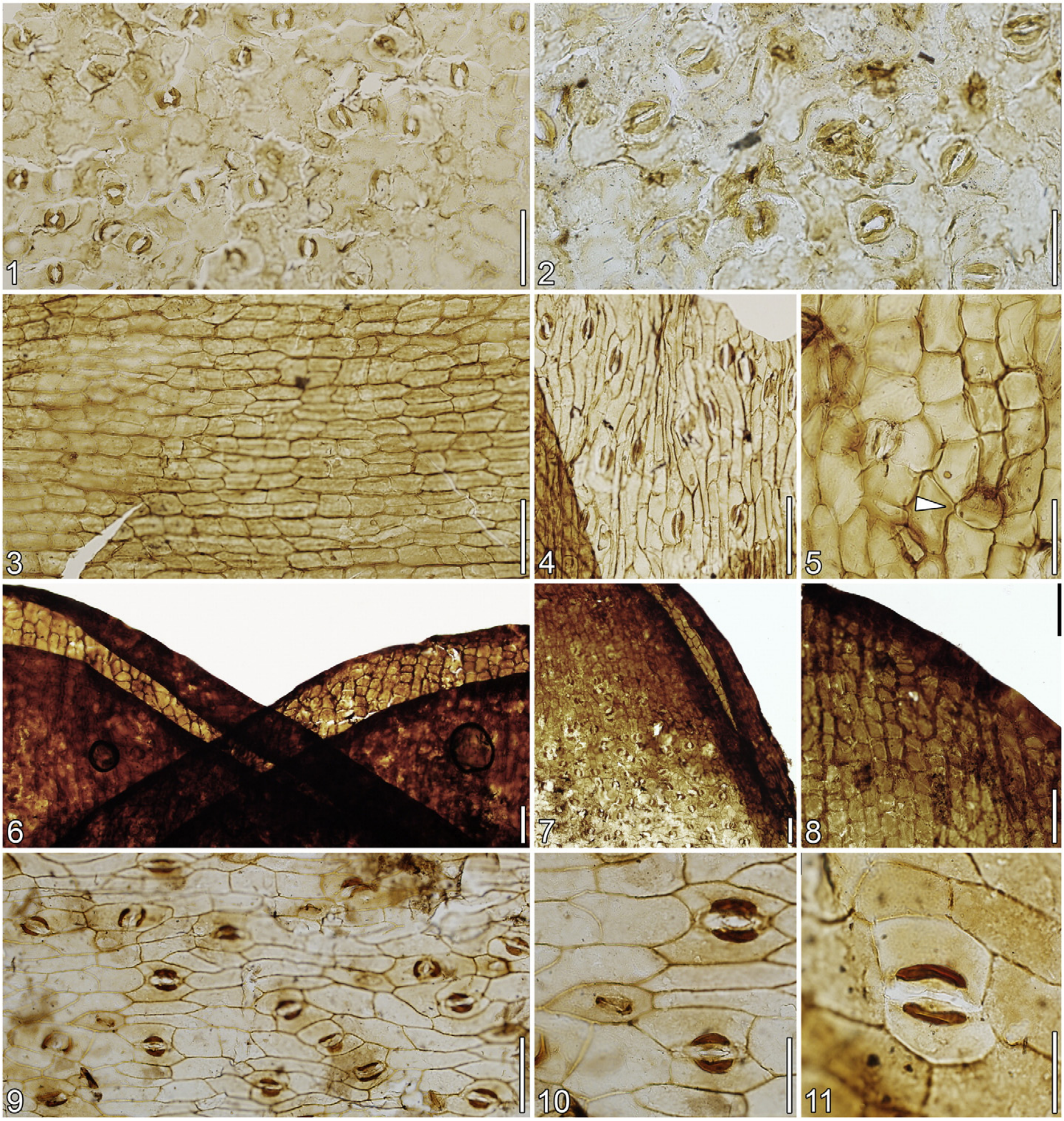

Plate VII. Cuticles of *Wielandiella* and *Welsbergia* from the Rhaetian of Wüstenwelsberg. 1. *Wielandiella angustifolia*, leaf, abaxial cuticle, Q677/08-01, 100 μm. 2. *Wielandiella angustifolia*, leaf, abaxial cuticle, Q671/08-01, 50 μm. 3. *Wielandiella angustifolia*, bract, abaxial cuticle, Q638/08-05, 100 μm. 4. *Wielandiella angustifolia*, bract, adaxial cuticle, 132wü02-01, 100 μm. 5. *Wielandiella angustifolia*, bract, adaxial cuticle with hair bases (*arrowhead*), Q638/08-01, 50 μm. 6. *Welsbergia bursigera*, apices of microsporophylls, Q809/08-01, 100 μm. 7. *Welsbergia bursigera*, outer cuticle of microsporophyll, Q809/08-05, 100 μm. 8. *Welsbergia bursigera*, outer cuticle of microsporophyll, Q809/08-07, 100 μm. 9. *Welsbergia bursigera*, inner cuticle showing stomatal distribution, Q809/08-04, 100 μm. 10. *Welsbergia bursigera*, inner cuticle (detail of Plate VII, 9), Q809/08-04, 50 μm. 11. *Welsbergia bursigera*, inner cuticle, detail of a stoma, Q809/08-08, 10 μm.

928/13–931/13, 965/14, 968/14, 971/14; 12wü02, 25wü02, 28wü02, 30wü02, 32wü02, 52wü02, 55wü02, 61wü02(c), 63wü02, 65wü02, 86wü02, 89wü02, 104wü02, 107wü02, 110wü02, 120wü02, 121wü02, 127wü02, 134wü02, 139wü02, 158wü02, 172wü02, 38wü03, 52wü03, 61wü03, 66wü03, 78wü03, 80wü03, 95wü03, 111wü03, 129wü03, 134wü03, 08wü04, 12wü04, 21wü04(c), 28wü04, 29wü04, 36wü04(c), 39wü04, 40wü04, 49wü04, 04wü05, 07wü05, 03wü08, 21wü08, 60wü08, 63wü08, 65wü08, 72wü08, 81wü08, 88wü08(c), 98wü08, 101wü08, 102wü08, 112wü08, 171wü08, 83wü09, 99wü09, 109wü09, 07wü11, 17wü11, 19wü11, 06wü12, 10wü12, 23wü12, 07wü13, 09wü13. *Bracts*: Q330/3, 331/03(c), 638/08(c), 639/08, 827/10, 828/10; 29wü08, 53wü08, 111wü08. *Ovulate organ*: 132wü02(c).

WELSBERGIA C.Pott et Van Konijnenb. *gen. nov.*

Type: *Welsbergia bursigera* (Harris, 1932b) comb. nov., from the Rhaetian (Upper Triassic) of Jameson Land, Greenland (see Harris, 1932b), and Wüstenwelsberg, Bavaria, Germany.

Diagnosis: Bennettitalean microsporophyll consisting of several thin and straight, longitudinally wrinkled axes originating from a petiole and diverging at a low angle forming a steep conical shape. Each axis carries two rows of capsules, here interpreted as pollen sacs comprised of two semi-circular valves adnate in their lower (basal) half, but separate along the margin in the rounded area. Pollen sacs attached laterally to the axes by their full width and bent perpendicularly to the axis towards the centre of the reproductive structure. Outer (lower) cuticle very robust, epidermal cells with prominent, straight periclinal and smooth anticlinal walls. Cells arranged in well-defined, longitudinally oriented rows. Stomata of the brachyparacytic type, diacytic and arranged within the cell rows, usually covering several adjacent rows. Inner (upper) cuticle delicate and thinly cutinised. Epidermal cells narrow and arranged in long rows. Epidermal and subsidiary cells with skewed short edges, forming acute angles. Periclinal walls straight; anticlinal walls smooth. Stomata of the same structure, organisation and composition as those from the outer surface, but their shape differring with the subsidiary cells, short in length but great in width.

Etymology: After Wüstenwelsberg, where the specimens that necessitated the erection of the new genus have been found.

Fig. 2. Restoration of *Welsbergia bursigera* from the Rhaetian of Wüstenwelsberg, with a few leaves of *Pterophyllum aequale* indicated in the background. Illustration by Pollyanna von Knorring, Stockholm, Sweden.

Remarks: Based on the expanded knowledge of the architecture, organisation and structure of this fructification from the specimens studied here, we erect the new genus *Welsbergia*. *Bennettistemon*, to which the original specimens from Jameson Land were assigned, lacks any clear affiliation of its 'species' except for "microsporophylls which can be referred to Bennettitales, but which are imperfectly known" (Harris, 1932b, p. 98). *Bennettistemon bursigerum* is no longer 'imperfectly known' and, consequently, the new specimens necessitated the erection of a new genus to accommodate these bennettitalean microsporophylls.

Welsbergia bursigera (Harris, 1932b) comb. nov.
Plate IV, 8–11, Plate VII, 6–11, Fig. 2.

Synonymy and references:

1932b *Bennettistemon bursigerum* — Harris, p. 99; pl. 12, figs 5–10; pl. 13, figs 1–4, 10.
1937 *Bennettistemon bursigerum* Harris — Harris, p. 53; no illustration.
1950 *Bennettistemon bursigerum* Harris — Lundblad, p. 66; pl. 11, figs 6–12; pl. 12, figs 5–6; text-fig. 27.
2014 *Bennettistemon bursigerum* Harris — Pott, p. 488; text-fig. 17.

Holotype: Slide 1652, figured by Harris (1932b) on pl. 12, fig. 6; stored at the Natural History Museum of Denmark (NHMD), Copenhagen.
Epitypes: 28wü09, 77wü09 (Plate IV, 8, 9).
Type locality: Astartekløft, Jameson Land, East Greenland.
Type horizon and age: *Lepidopteris* Bed, Kap Stewart Formation; Rhaetian, Upper Triassic.

Remark on types: Specimen 1652, published by Harris (1932b, pl. 12, fig. 6), automatically becomes the holotype of the new combination and the new genus. This specimen, however, is too fragmentarily preserved to reflect the structure of the entire organ and we, therefore, chose specimens 28wü09 and 77wü09 as epitypes to serve as interpretative types yielding the most complete organs preserved (Plate IV, 8, 9).

Emended diagnosis: Microsporophyll consisting of several thin and straight axes originating from a petiole and diverging at a low angle to form a steep conical shape; each of the axes carrying two rows of semi-circular capsules, here interpreted as pollen sacs consisting of two valves. Valves usually remaining together after dehiscence. Outer (upper) cuticle of valves quite thick near free margin, becoming delicate towards base, showing polygonal straight-sided cells without median papillae. Stomata common near base of capsule, but absent towards free margin. Guard cells oriented arbitrarily. Subsidiary cells unspecialised and less cutinised than epidermal cells, guard cells with strongly developed curved cutin thickenings. Inner (lower) cuticle of valve delicate, showing elongate straight-sided cells with distinctly skewed short ends. Subsidiary cells much wider than long; guard cells of same type as those in upper cuticle, but all oriented longitudinally. Pollen sac lined by a granular, non-cellular cuticle. Pollen grains oval, 24 × 15 μm, with smooth walls and having a longitudinal fold or slit (emended after Harris, 1932b, and adapted to our findings).

Description: The specimens assigned here to *Welsbergia bursigera* all have a similar reproductive structure consisting of several thin and straight axes that are longitudinally wrinkled. The number of axes is not unambiguously determinable, but some specimens have at least ten. The axes originate from a petiole that has a similar surface structure, and they diverge at low angles, forming a steep conical shape. Each of the axes carries two rows of semi-circular pollen sacs over its full length. The pollen sacs consist of two valves that are adnate in their lower (basal) half, but separate along the margin in the rounded area. The pollen sacs are attached laterally to the axes by their full width and then bent perpendicularly to the axis towards the centre of the reproductive structure (Plate IV, 8–11, Fig. 2).

The cuticle of the pollen sacs can be differentiated as deriving from the upper and lower epidermis. We here interpret the more robust one as the outer (lower) cuticle that protects the whole structure, and the delicate one as the inner (upper) cuticle. The outer cuticle is more robust; the epidermal cells have prominent, straight periclinal and smooth anticlinal walls. The cells are arranged in well-defined, longitudinally oriented rows. Although their width is consistently retained, the length of the rectangular cells decreases continuously from the base of the pollen sac towards the edge. The latter cells are almost isodiametric, whereas the former are elongate. All cells have end walls that are more or less perpendicular to the side walls or are arranged at a low angle. A few stomata occur, regularly scattered along the complete surface of the outer epidermis of the pollen sac. The stomata are of the brachyparacytic type, diacytic and arranged within the cell rows; however, they usually expand over several adjacent rows. The stomata are arbitrarily oriented; their subsidiary cells are less strongly cutinised than the surrounding epidermal cells, and commonly as long as wide or longer than wide; the guard cells, especially the dorsal walls of the crescent portions, are strongly cutinised (Plate VII, 6–8).

In contrast, the inner cuticle is very delicate and the epidermis was only thinly cutinised. The epidermal cells are very slender and arranged in similar long rows as in the outer cuticle, but the cells are much longer and thinner, giving the whole cuticle a delicate appearance. Their length decreases similarly towards the margin of the pollen sac, but not as prominently as in the outer epidermis. A striking difference is that all epidermal and subsidiary cells exclusively have skewed polar ends forming acute angles. The periclinal walls are straight and the anticlinal walls are smooth. The stomata are common; their number appears as high as the number of normal epidermal cells. They are of the same structure, organisation and composition as those from the outer surface. However, their shape differs as the subsidiary cells are short but very wide, 'adapted' to or 'shaped' by the long and slender epidermal cells, because the stomata are always oriented with the pit perpendicular to the rows formed by the cells. Through this, the stomatal complexes extend only over two of the cell rows. No trichome or hair bases, papillae or other epidermal and cuticular features were observed on either cuticle. The cuticles from the axes of the reproductive structure are poorly preserved; small portions suggest that the epidermis was of a similar organisation and structure as the lower epidermis of the pollen sacs (Plate VII, 9–11).

Harris (1932b) mentioned sporangia that he identified within the capsules (here interpreted as pollen sacs), which were lined by a granular, non-cellular cuticle. Here, we have no evidence of such sporangia, but, in every cuticle preparation made from the pollen sacs, such a granular, non-cellular cuticle appeared, although it was impossible to recognise any structure in the appearance of this very thin cuticle.

Measurements: The longest and most complete specimen is 98.4 mm long; another one measures 79.4 mm in length. The petiole extends to a maximum width of 8.1 mm; its preserved portion is 13.2 mm long. Apically, the diverging pollen sac-carrying rays widen to an area 20.3 mm wide; the second specimen mentioned earlier reaches 13.6 mm wide. The pollen sacs have a basal width of 3.8–4.3 mm and 1.8–2.4 mm long.

Remarks: Unfortunately, no sampled specimens bore any pollen grain (or any hint for individual sporangia). This implies that all examples had released their pollen and that those structures were subsequently shed as a whole. This also requires re-interpretation of an earlier determination of conspecific structures from Jameson Land (Harris, 1932b). We assigned the specimens from Wüstenwelsberg to *Bennettistemon bursigerum*, because the bivalved pollen sacs are conspecific with the structures that Harris (1932b) reported from Jameson Land, for which he erected this name. Harris (1932b) apparently found only the apical portions of the pollen sacs, calling them bivalved synangia, providing apparently internal structures that he interpreted as sporangia. The latter have not been observed thus far. Harris (1932b) missed what he called 'inner cuticle' probably because of its delicate character. The description of the 'outer cuticle' by Harris (1932b) agrees with the one we also regard as the outer cuticle. Harris (1932b) also found small spores (pollen) with smooth walls and a longitudinal fold or slit. The specimens from Wüstenwelsberg now clarify the entire structure of the pollen organ or microsporophyll (Harris, 1932b); in addition, they expand our knowledge of the species to such an extent that we consider that they can no longer be accommodated in *Bennettistemon* and require assignment to a new genus. We have chosen to name it *Welsbergia* after the quarry of Wüstenwelsberg and the species is consequently named *W. bursigera*.

All specimens of *Welsbergia bursigera* occur in a single layer (level 2, see Material and Methods) hosting a large and almost monospecific assemblage of *Pterophyllum aequale* leaves. Moreover, *W. bursigera* remains are commonly preserved on the same hand specimens and in close association to *P. aequale* leaves, indicating their probable biological affinity. This is also the case with the Jameson Land material; Harris (1932b, p. 100) mentioned a "commonest association" with the same foliage (*P. schenkii* in Harris, 1932b; see Pott and McLoughlin, 2009). The close association of abundant shed foliage of *P. schenkii* and *W. bursigera* strongly argues for that both plant organs derive from the same parent plant.

Considering the position and function of this fructification, it is difficult to determine whether it was pendulous or erect on a branch. A pendulous interpretation is favoured by its delicate appearance with the long, thin axes (pointing to wind-dispersal of the pollen), whereas an upright arrangement is supported by the very stiff appearance of the shed organs and the completeness of the preserved portions (pointing to wind- or insect-pollination).

The possible ovulate organ: Many vascular plants, especially gymnosperms and many angiosperms, have separate reproductive structures, not only into discrete male and female organs (monoecism), but also,

Table 1
Comparison of macromorphological and epidermal anatomy of the *Pterophyllum aequale*/*Welsbergia bursigerum* plant and *Wielandiella angustifolia*.

	Pterophyllum aequale/Welsbergia bursigerum	*Wielandiella angustifolia*
Leaf architecture	Regularly segmented, impari-pinnate	Regularly segmented, pari-pinnate
Leaf size (length × width; assumed full length)	14.8 × 5.3 cm; 20–22 cm	17.1 × 2.5–2.8 cm; 20–25 cm
Leaflets	Inserted at right angles, parallel-sided, narrow, linear, not tapering, obtusely rounded apically with small central notch; size: up to 28 × 3–7 mm	Inserted at almost right angles, falcate with one concave and one convex margin, tapering towards apex, rounded apically without any notch; size: up to 13–14 × 5–8 mm
Leaf venation density	20–22 veins/cm	18–20 veins/cm
Epidermal anatomy	Hypostomatic, brachyparacytic and diacytic stomata restricted to lower (abaxial) epidermis Arrangement, orientation, size of epidermal cells, etc. similar in both species	
Stomata	Presence of a central papilla characterizing the subsidiary cells, normally cutinised dorsal cell walls of the subsidiary cells	Absence of a central papilla on the subsidiary cells, strongly cutinised dorsal cell walls of the subsidiary cells
Cell walls	Straight anticlinal cell walls; periclinal cell walls with a central solid cuticular thickening	Sinuous anticlinal cell walls; periclinal cell walls smooth
Papillae	Apart from those of the subsidiary cells free of papillae	Loosely distributed hollow papillae on abaxial epidermis

Table 2
Synopsis of key taxa and bennettitalean taxa in different Rhaetian floras from the Northern Hemisphere (see also Fig. 3). The colour scheme indicates shared taxa in the different floras.

Rhaetian taxa	Jameson Land	Franconia	Scania	S Poland	Donets	Alborz
Key taxa:						
Clathropteris meniscioides	X	X	X		X	X
Ctenis fallax	X	X	X	X		
Dictyophyllum exile (or *D. nervulosum*)	X	X	X	X	X	X
Equisetum muensteri	X		X	X		
Hydropterangium marsilioides	X	X	X		X (cf.)	
Lepidopteris ottonis	X	X	X	X	X	X
Marattia intermedia	X	X	X	X		X
Neocalamies lehmannianus	X		X	X	X	X (sp.)
Phlebopteris angustiloba	X	X	X	X		X
Phlebopteris muensteri	X	X	X	X		
Ptilozamites nilssonii/P. heeri	X	X	X			
Stachyotaxus septentrionalis (incl. *S. elegans*)	X	X	X	X		
Taeniopteris tenuinervis	X		X	X		
Thaumatopteris brauniana	X	X	X	X		X
Thaumatopteris schenki	X		X	X		
Todites goepppertianus (*T. williamsonii*)	X	X (sp.)	X	X	X	X
Bennettitales:						
Anomozamites amdrupiana	X					
Anomozamites hartzi	X					
Bennetticarpus crossospermus	X					
Bennetticarpus exiguus	X					
Bennetticarpus oxylepus	X					
Bennetticarpus tylotus	X					
Bennettistemon amblum	X					
Bennettistemon ovatum	X					
Otozamites sp. A	X					
Pterophyllum hanesianum	X					
Pterophyllum rosenkrantzi	X					
Pterophyllum xiphipterum	X					
Pterophyllum zygotiacum	X				X (sp.)	
Taeniozamites groenlandica	X					
Vardekloeftia sulcata	X					(X)
Otozamites bechei						
Otozamites obtusus				X		
Nilssoniopteris ajorpokensis	X	X				
Nilssoniopteris jourdyi	X	X				
Pterophyllum astartense	X	X				
Pterophyllum kochii	X	X				
Pterophyllum pinnatifidum	X	X				
Anomozamites gracilis	X	X	X			
Pterophyllum aequale	X	X	X		X	X (cf.)
Welsbergia bursigera	X	X	X			
Wielandiella angustifolia	X	X	X		X[1]	X[1]
Pterophyllum ptilum	X		X		X (cf.)	
Pterophyllum subaequale	X		X	X		
Anomozamite intermedium			X			
Anomozamites minor			X			
Anomozamites triangularis			X		X (sp.)	
Pterophyllum irregulare			X	X		
Pterophyllum majus			X			X
Zamites corrugatus					X	
Anomozamites polymorpha						X
Dictyozamites asseretoi						X
Nilssoniopteris mikailovii						X
Nilssoniopteris musafolia						X
Nilssoniopteris schenkiana						X
Otozamites furoni						X
Pterophyllum bavieri						X
Pterophyllum cf. *P. filicoides*						X
Pterophyllum cf. *P. firmifolium*						X
Pterophyllum nathorsti						X
Pterophyllum schenki						X[2]
Pterophyllum tietzei						X
Zamites persica						X
Sources for bennettitalean taxa	Harris (1932b); Pedersen et al. (1989)	This study	Pott and McLoughlin (2009, 2011); Lundblad (1950); Pott (2014a)	Raciborski (1891); Reymanówna (1963); Barbacka et al. (2014)	Stanislavski (1971)	Schweitzer and Kirchner (2003)

[1] Sterile foliage only
[2] Not *Pterophyllum aequale*

in many cases, allocated to separate individual organisms (dioecism). This involves sexual dimorphism visible in the different female and male plants, especially in their reproductive structures. Several gymnosperms, such as *Ginkgo biloba*, various yews (Taxaceae), some junipers (Cupressaceae), several gnetaleans (*Gnetum*, *Ephedra*, *Welwitschia*), many araucarians and all cycads (Cycadales), display dioecism, that is, female and male reproductive organs are produced on separate plants. These plants differ in the structure, architecture, organisation and positioning of their reproductive structures. However, how far the sexually induced dimorphism extends is hard to determine, because in all species known to us this is restricted to the reproductive structures only and does not involve any other organs, such as axes, stems or foliage. Therefore, the following hypothesis, even if being a very intriguing question, is at present hard to verify, but hopefully will stimulate further discussion.

The epidermal architecture of *Welsbergia bursigera* is more similar to that of the bracts and sterile leaves of *Wielandiella angustifolia* than to that of *Pterophyllum aequale*, the foliage type with which *Welsbergia bursigera* is always confidently associated in several localities. *P. aequale* is distinguished from foliage of *Wielandiella angustifolia* by the shape and outline of its leaflets, as well as by the shape of the epidermal and the guard cells (Table 1; see Pott and McLoughlin, 2009). However, in some cases, identification based on macromorphology failed and a cuticle sample was necessary to prove the identification, implying a very close relationship between the two foliage types.

Due to these facts, the question arose whether a plant bearing *Pterophyllum aequale* foliage and *Welsbergia bursigera* microsporangia could be the male plant of a species of which *Wielandiella angustifolia* is the female plant, despite the mentioned differences displayed in the two types of foliage. This would include a sexual dimorphism in male and female plants that is not restricted to the reproductive structures alone, but also involving other plant organs, in this case, sterile foliage. This can, however, not be verified and we are not aware of any example in modern day flora where dioecious plants display a sexual dimorphism that involves more plant organs than the reproductive structures alone. Sterile leaves of male and female plants in the earlier mentioned *Ginkgo biloba* tree, in dioecious yews and junipers, as well as in all cycads are, for example, not distinguishable.

In fact, habitat- or location-related environmental influences or factors have usually a much higher impact on leaf shape and structure (such as, e.g., sunny or shady habitats, altitude, physiological drought, etc.) than any other factors (Parkhurst and Louks, 1972; Napp-Zinn, 1988). The differences in the epidermal and cuticular anatomy of both species may indicate this. Leaves and microsporophylls of the *Pterophyllum aequale* plant have never been found intermixed with leaves of the *Wielandiella* plant, which indicates that both plants were not growing at the same locations, probably experiencing different environmental influences that may cause different leaf shapes and structures, but may not affect the reproductive structures. This fact would also lead to a discussion of a potential pollinator (wind versus animal) favouring wind-pollination for *W. angustifolia*; in contrast, gland-like structures on the immature ovulate organs of the latter, for example, have recently been interpreted as substance-producing to attract animal pollinators (Pott, 2014a).

It has earlier been argued that most members of the Williamsoniaceae had their micro- and macrosporangia in separate reproductive organs, either on the same plant or on different plants (Schuster, 1911; Harris, 1932b, 1969; Crane, 1988; Watson and Sincock, 1992; Pott et al., 2010; Pott, 2014a; Pott and McLoughlin, 2014), except for the bisexual *Williamsoniella* (Thomas, 1915; Harris, 1944, 1969), whereas members of the Cycadeoidaceae always produced bisexual reproductive structures (e.g., Wieland, 1916; Delevoryas, 1968; Crepet, 1974; Crane, 1988). Assuming a dioecious nature for the *Wielandiella*/*Pterophyllum aequale*-plant species is, consequently, not too devious, but solid evidence for this hypothetic scenario is hard to provide.

Material examined: Q747/09, 748/09, 767/09, 798/09, 805/09–808/09, 809/09(c), 810/09, 820/10, 821/10, 951/14, 980/15, 981/15, 984/15, 988/15, 989/15; 28wü09, 30wü09, 33wü09, 36wü09–38wü09, 73wü09, 75wü09–77wü09, 113wü09; UU23310, 24440.

4. Discussion

4.1. Composition of the flora

The Rhaetian of from Wüstenwelsberg is currently under detailed study by the authors and its composition cannot yet be fully resolved (Bonis et al., 2010). Similarly, the nearby Rhaetian florule of Heilgersdorf has not been fully documented (Kelber and Van Konijnenburg-van Cittert, 1997). Wüstenwelsberg appears to have supported a particularly diverse Rhaetian flora. Besides the here studied members of Bennettitales, other plants in the flora include one club moss (*Selaginellites coburgensis*; Van Konijnenburg-van Cittert et al., 2014), two *Equisetites*-type horsetails, nine to ten fern and seven seed fern taxa, about seven types of cycadophyte foliage attributable to Cycadales and Nilssoniales, about three conifer-taxa (some with cones) and two ginkgophyte taxa (see also Bonis et al., 2010). The Bennettitales in the Wüstenwelsberg flora constitute one of the dominant components of this flora. We recognised eight bennettitalean foliage types, one of which is the foliage of *Wielandiella angustifolia*, recently restored as a whole plant by Pott (2014a, 2014b). In addition, we found immature ovulate organs and bracts of *Wielandiella angustifolia*. The most notable determination is, however, a new type of bennettitalean microsporophyll, for which we erected *Welsbergia*, with its type species *Welsbergia bursigera*. *Welsbergia bursigera* is exclusively associated with foliage of the *Pterophyllum aequale*-type.

4.2. Comparisons

4.2.1. Comparison with other Rhaetian–Hettangian floras from the Northern Hemisphere

The Wüstenwelsberg flora incorporates key Rhaetian taxa, such as *Dictyophyllum nervulosum*, *Equisetum muensteri*, *Marattia intermedia*, *Phlebopteris angustiloba*, *Phlebopteris muensteri*, *Ptilophyllum heeri*, *Thaumatopteris brauniana*, *Thaumatopteris schenkii* and *Lepidopteris ottonis*. Typical bennettitalean taxa include *Wielandiella angustifolia*, *Anomozamites gracilis* and *Pterophyllum aequale* (Table 2). These species are shared with the renowned Rhaetian floras from Jameson Land (Harris, 1926, 1931, 1932a, 1932b, 1935), Scania (Nathorst, 1878–1886; Pott and McLoughlin, 2009, 2011; Pott, 2014a), Poland (Barbacka et al., 2014a, 2014b), the Donets Basin (Stanislavski, 1971) and Alborz (Schweitzer and Kirchner, 1995, 1996, 1998, 2003; Schweitzer et al., 1997, 2000, 2009) (Table 2).

However, there are notable differences. The floras of Jameson Land and Scania differ especially in the composition of the bennettitalean component. The Jameson Land flora comprises 26 bennettitalean taxa, whereas only eleven have been recorded from Scania. Only six of these 31 taxa are shared by these floras (Table 2). The flora from Wüstenwelsberg shares more taxa (nine) with the Jameson Land flora than with the generally closer flora from Scania (four), all of which also occur in Jameson Land (Table 2). Additionally, the Scanian floras share a few taxa with those from Poland that have not been recorded from Franconia. The causes for these differences are difficult to assess and may be related to local environmental influences (see later). A flora expected to have a very similar composition to the Wüstenwelsberg assemblage is the Rhaetian flora from south-central Poland, but, unfortunately, the bennettitalean component is rather poor (Barbacka et al., 2014a, 2014b). The Rhaetian flora from Wales (Swift, 1999) is poor in species diversity and therefore has less significance here.

Fig. 3. Palaeogeographical map of Europe and eastern Asia during the Rhaetian, indicating the Rhaetian plant assemblages known so far. The shaded area marks a latitude of ca. 40°–50° N. Base map by Ron Blakey, Colorado Plateau Geosystems Inc., Flagstaff, AZ, USA.

Floras further to the east, such as those from the Donets Basin and Alborz in Iran (Fig. 3), share respectively fewer taxa with the central European Rhaetian floras (Table 2). Moreover, they possess taxa (e.g., *Pterophyllum nathorstii*, *P. schenkii* or *P. tietzei*) that are absent from western European floras. Very few of the central European bennettitalean taxa expanded their range to these eastern floras. Sterile foliage of *Wielandiella angustifolia* and the foliage type *P. aequale* have been recorded from the Donets Basin and Alborz, two taxa that also are present in all European floras, and thus they can be regarded as key taxa for Rhaetian floras. In general, however, each flora hosts its own distinctive assemblage of bennettitalean taxa. Rhaetian bennettitalean assemblages appear to have been strongly provincial in contrast to examples from, for example, Carnian or Hettangian floras of the same areas (Barbacka, 2000; Schweitzer and Kirchner, 2003, and references therein; Pott and McLoughlin, 2009, 2011, and references therein; Pacyna, 2013; Pott, 2014b; Bauer et al., 2015, and references therein; Pott and Launis, 2015).

Rhaetian floras in Europe and the Middle East are usually closely associated with Hettangian floras such as Scania (Pott and McLoughlin, 2009, 2011), southern Germany (Schenk, 1865–1867; Gothan, 1914; Weber, 1968; Kirchner, 1992; Van Konijnenburg-van Cittert, 1992), south-central Poland, (Pacyna, 2013; Barbacka et al., 2014a, 2014b) and Alborz, Iran and Afghanistan (Schweitzer and Kirchner, 1995, 1996, 1998, 2003; Schweitzer et al., 1997, 2000, 2009). The general composition of those floras did not change too dramatically at the Rhaetian–Hettangian boundary. However, some localities at which Rhaetian–Hettangian floras have been described, are, in fact, exclusively Hettangian or younger, amongst which are the floras of the Mescek mountains in Hungary (Barbacka, 2000) and south-central Romania (e.g., Popa and Van Konijnenburg-van Cittert, 2006; Popa, 2009).

4.2.2. Comparison with the Hettangian flora of Franconia

The Rhaetian flora of Wüstenwelsberg markedly differs from the Hettangian flora of adjacent areas in Franconia (see Van Konijnenburg-van Cittert et al., 2014, and references therein). All major plant groups are present, but the species and even genera within the two floras contrast considerably. The ferns are the only group in which six species are shared by the Rhaetian and in the Hettangian floras. Of those, *Clathropteris meniscoides* is common in Wüstenwelsberg and rare in the Hettangian flora. Both floras contain about ten fern species, partly of the same genera, but with different species; in the Hettangian floras, *Selenocarpus*, *Goeppertella* and *Phialopteris* are present but not in the Rhaetian flora. All three fern genera have relatively delicate fronds, so this might explain their absence in the Rhaetian flora that is interpreted to be more allochtonous.

The horsetails have one species in common (*Equisetites muensteri*); club mosses are completely absent in the Hettangian floras. The most obvious difference is in the seed ferns, as the index fossil species *Lepidopteris ottonis* (very common in Wüstenwelsberg) disappears completely prior to the Hettangian. The Caytoniales appear for the first time, and corystosperms, which are rare in the Rhaetian, become common in the Hettangian floras. The number of cycad species in both floras is more or less the same, but the difference is in the representation of taxa. In both floras, *Nilssonia* occurs, but is represented by different species; *Ctenis* (and possibly also *Pseudoctenis*) are common in the Rhaetian flora, but absent in the Hettangian; and *Cycadites* appears in the Hettangian together with *Cycadospadix*, but is absent in the Rhaetian flora.

The most obvious difference is recognisable in the Bennettitales. Wüstenwelsberg yields a very diverse bennettitalean flora, whereas there is only one species in the Franconian Hettangian flora that is common (*Otozamites brevifolius*, which has been found associated with *Weltrichia*). *Pterophyllum*, *Anomozamites* and *Nilssoniopteris* occur in the Hettangian flora, but these taxa are very rare. The Ginkgophyta are represented by one species, viz. *Ginkgoites taeniatus*, which appears in the uppermost beds of Wüstenwelsberg and is common in the Hettangian. Additionally, the Hettangian floras include the ginkgoalean taxa *Sphenobaiera spectabilis* together with *Karkenia*, *Schmeissneria* *microstachys* (with *Stachyopitys preslii*; Kirchner and Van Konijnenburg-van Cittert, 1994) and czekanowskialean leaves. The latter might be present in the Rhaetian flora as well, but have not yet been studied. The representation of conifers in these floras is also different; only *Schizolepis liasokeuperianus* is present in both floras, but as the Rhaetian flora includes *Stachyotaxus* and *Elatocladus* shoots associated with female cones, the Hettangian one contains *Hirmeriella muensteri* (Clement-Westerhof and Van Konijnenburg-van Cittert, 1991). Moreover, two *Podozamites* species and one *Palissya* species are common in the Hettangian floras. Finally, *Desmiophyllum gothanii* with its male (*Piroconites*) and female (*Bernettia*) fructifications occurs in the Hettangian — possibly a gnetalean taxon.

4.3. Ecological implications

All Rhaetian floras mentioned earlier were located at a palaeolatitude of around 40°–50° N (Fig. 3). From this point of view, similarities in their composition are to be expected (see Table 2). However, it has been argued recently (for the Carnian and the Berriasian) that different longitudinal position has much more significant influence on floral composition than latitudinal position (Pott, 2014b; Pott et al., 2014). This effect can also be recognised in Rhaetian–Hettangian floras of Europe and the Middle East. The floras examined here were all positioned at almost equivalent latitudes but spread through 60°–70° of longitude (Fig. 3).

A major cause of this effect is most likely tectonic events; not only the initial breakup of Pangaea and the drifting apart of Laurasia and Gondwana in the late Triassic period. The incipient formation of the Atlantic Ocean (the Laurasian Transcontinental Seaway) through the breakup of Laurasia, might have created a rapidly changing environment of channels and islands with a highly sophisticated system of cold and warm water currents with related up- and down-winds and micro-habitats between the land areas that later became Greenland and Scandinavia on one side and a heavily subdivided archipelago to become Central Europe (UK, Germany, Poland, Hungary, Romania) on the other side.

Bennettitaleans are seed plants that are interpreted to have thrived predominantly in deltaic and highly disturbed environments (Harris, 1932b, 1969; Pott et al., 2008b, 2012, 2014, 2015; Pott and McLoughlin, 2009, 2011, 2014; Pott, 2014a, 2014b). Thus, they were susceptible to changing coastal conditions (Fig. 3). Their advanced reproductive capability probably allowed these plants to quickly adapt to new environmental challenges that led to the differences in the composition of these floras, whereas other deltaic or moist-environment-related plant groups, such as the spore-reproducing club mosses, horsetails and ferns account for the superficial similarity of these floras because of their wide dispersive adaptive potential. A similar scenario of a fragmented palaeogeographic and rapidly changing environment in a small area during the end of the Late Triassic and Early Jurassic has been observed by Kiritchkova and Nosova (2014) in the Middle Caspian Basin, also hosting a flora dominated by similar bennettittalean taxa.

The lesser distance between the palaeolocations of the Scanian and Franconian floras compared to the more remote Jameson Land flora would lead to the expectation that both floras would share a high number of bennettitalean taxa. However, the flora of Wüstenwelsberg is comprised of a higher number of 'Greenlandic' than 'Scanian' bennettitalean taxa. The only taxa that Wüstenwelsberg shares with Scania are present in Jameson Land as well (Table 2). The explanations for these different compositions might be ecological. One conceivable scenario might involve the cooler Arctic waters (with their higher density) flowing southwards through the Laurasian Transcontinental Seaway (Koch and Viking straits; Fig. 3) between the land areas of Greenland and Scandinavia into the warmer Tethys Ocean (Bjerrum et al., 2001). Accompanying northerly trade winds account for the dispersal and reception of seeds and pollen from Jameson Land with a higher ratio to Franconia than to Scania, whereas from Scania, dispersal was directed more eastward than southwards, towards the floras from Poland that share some bennettitalean taxa with Scania, which are not recorded from Franconia (Pacyna, 2013; Barbacka et al., 2014b, 2015). Water currents and winds might also cause similarities in the abiotic environmental influences that plants would be affected by in the more exposed Jameson Land and Franconia areas; Scania and southern Poland would have less exposed areas due to their more protected leeward location (see Bjerrum et al., 2001). In our view, the various connections between the different habitats resulting in the similarities and differences in the bennettitalean communities of the different floras might be explained by water currents and winds.

Barbacka et al. (2015) recently carried out a statistical analysis of European Jurassic floras. The authors found that differences in environmental conditions resulting from geographic and topographic factors explain differences between adjacent floras (Hungary: deltaic environment; Romania: intramontane depression filled by a braided river system). The remarkable difference in the composition of the Bennettitales from the Rhaetian and Hettangian floras of Franconia may thus indicate local environmental changes. Similar changes do not occur in other Rhaetian–Hettangian floras (Harris, 1937; Pott and McLoughlin, 2009; Pacyna, 2013, 2014).

Further reasons for such differences might involve different salinities of the ground waters, osmotic potentials of the soils and other locally induced factors affecting plants in their local habitats, such as heavy rain or consistent winds. These are, however, less likely because the different biotic and abiotic environmental influences would induce differences in epidermal or cuticular anatomy. As no differences have been observed in the macroscopic and microscopic leaf architecture between members of the same species from different floras, these factors most likely can be excluded (compare, e.g., Harris, 1932b; Pott et al., 2008a; Pott and McLoughlin, 2009, 2011; Pott, 2014b).

5. Conclusions

The bennettitalean plant remains from the Rhaetian of Wüstenwelsberg, Franconia, southern Germany, are highly diverse. Eight species of *Pterophyllum* (4 species), *Anomozamites* (1 species), *Nilssoniopteris* (2 species) and *Wielandiella* (1 species with sterile leaves, bracts, ovulate reproductive structures) have been identified. In addition, an enigmatic type of clearly bennettitalean (confirmed by its cuticle) microsporangiate reproductive structure has been obtained, remains of which from the Rhaetian of Greenland had been assigned to *Bennettistemon*. The material from Wüstenwelsberg, however, is much more complete and required, due to its very unique architecture amongst bennettitaleans, the erection of a new genus, viz. *Welsbergia* gen. nov. The type species is *Welsbergia bursigera* comb. nov. *Welsbergia bursigera* reproductive structures are always exclusively associated with the sterile foliage *P. aequale*, and can, therefore, not be regarded as the microsporangiate organs of *Wielandiella angustifolia*, which is born by plants with sterile foliage of the *A. angustifolius*-type. The comparison of the Wüstenwelsberg flora with adjacent Rhaetian floras revealed distinct local differences in the bennettitalean component of the respective plant communities, which may have been a function of palaeogeographic factors and plant dispersal.

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