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Sphenophytes, pteridosperms and possible cycads from the Wuchiapingian (Lopingian, Permian) of Bletterbach (Dolomites, Northern Italy)

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ABSTRACT

The Bletterbach flora is the most important late Permian (Lopingian) flora of the Southern Alps. The study of a new fossiliferous bed stratigraphically below the cephalopod bed yielded almost 500 plant fossils, 28 of which belong to rare Lopingian plant groups: horsetails, seed ferns and possible cycads. Forty-five other fossils from the collection of Utrecht University were examined. The study of these more than fossils reveals a higher diversity of seed ferns and putative cycadophytes in the Lopingian of Europe than previously documented. Horsetails are represented by dispersed sporophylls, stem fragments and leaf sheaths too badly preserved for attribution to a species. Seed ferns are represented by *Sphenopteris* and the new genus *Germaropteris*, which includes *G. martinsii* (Germar in Kurtze 1839) Kustatscher, Kerp et Van Konijnenburg-van Cittert comb. nov., a species from the German Zechstein formerly assigned to various genera (e.g., *Callipteris*, *Lepidopteris*, *Peltaspermum*). Two species of *Sphenopteris* (*S. suessii*, *S.* sp.) are recorded for the first time from Lopingian strata of the Southern Alps. Remarkable are pinnae with alethopteroid pinnules, because similar forms have not been described from Lopingian deposits of Europe. Putative cycadophytes are represented by two taeniopterid leaves (*Taeniopteris* sp. A and *T.* sp. B) and a fragment of a pinnate cycad-like leaf. The Bletterbach flora is one of the most diverse European Lopingian floras, at least with regard to the non-conifer taxa. The floras of the Germanic Zechstein Basin and of the Southern Alps are more similar than previously considered, notwithstanding the vicinity of the latter region to the northern margin of the Palaeotethys; there are no obvious similarities to the floras that occurred along the southern margin of the Palaeotethys. In Europe, plant fossils are generally very rare in Lopingian strata and the presence of plant fossils in the Zechstein Basin and the Southern Alps is apparently related to sea-level changes. They appear to be most common immediately before and after the maximum transgression or sea-level high-stand.

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1. Introduction

The number of Lopingian ("late" Permian)[1] floras in Europe is very limited. Lopingian floras are known from the Zechstein Basin (British Isles, The Netherlands, Belgium, Denmark, Germany and Poland), from

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[1] We use the official terms Cisuralian, Guadalupian and Lopingian rather then the informal terms lower, middle and upper Permian; the latter are not well defined and have different meanings in various parts of the world.

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Hungary and the Southern Alps, northern Italy (see e.g., Chaloner and Meyen, 1973; Schweitzer, 1986). The floras from the Zechstein Basin are less diverse than Cisuralian ("early" Permian) floras and usually characterized by a dominance of conifers such as *Ullmannia* Göppert 1850, *Pseudovoltzia* Florin 1927 and *Quadrocladus* Mädler 1957 (e.g., Haubold and Schaumberg, 1985). The floras of the Southern Alps are dominated by conifers with *Ortiseia* Florin 1964 as major constituent and *Majonica* Clement-Westerhof 1987 and *Dolomitia* Clement-Westerhof 1987 as additional taxa (Visscher et al., 2001; Kustatscher et al., 2012). *Pseudovoltzia* and *Quadrocladus* are also known from the Southern Alps. Widespread, but much rarer additional elements include the pteridosperm genera *Sphenopteris* (Brongniart 1822) Sternberg 1825 and *Germaropteris* nov. gen., the putative pteridosperm or cycad *Taeniopteris* Brongniart 1828 and the ginkgophyte *Baiera* Braun 1846. *Germaropteris* is instituted here to include the Lopingian species *Germaropteris martinsii* (Germar in Kurtze, 1839) comb. nov., a species formerly assigned to various genera, such as *Callipteris* Brongniart 1849, *Lepidopteris* Schimper 1869 and *Peltaspermum* Harris 1937.

Several Cisuralian and Lopingian floras are known from the Southern Alps, northern Italy (e.g., Visscher et al., 2001). There are no unequivocal records of Guadalupian floras from this region; the Guadalupian is in Europe either represented by a hiatus, or developed in a redbed facies without plant fossils. The oldest Permian floras occur in the Collio Formation in the upper Trompia Valley (Sordelli, 1896; Remy and Remy, 1978) and the Tregiovo Formation of the upper Val di Non (Remy and Remy, 1978). These floras were dated as late Artinskian–Kungurian (late Cisuralian) based on palynostratigraphy and tetrapod footprints (Cassinis and Doubinger, 1991, 1992; Barth and Mohr, 1994; Visscher et al., 2001; Avanzini et al., 2011). Tetrapod footprints suggest a similar age for the flora from the Ponteranica Conglomerate near Gerola Alta, western Orobic Alps (Ronchi and Santi, 2003; Ronchi et al., 2005). The flora of the Gröden (or Val Gardena) Sandstone (formerly Grödner Sandstein; Italian: Arenaria di Val Gardena) is of Wuchiapingian (early–middle Lopingian) age (Kustatscher et al., 2012).

Seed fern foliage (*Sphenopteris*, callipterids) and seed fern or cycadophyte foliage (*Lesleya eckhardtii* (Germar in Kurtze 1839) Remy et Remy 1977) have been reported mostly from Cisuralian strata of the Southern Alps (e.g., Collio, Tregiovo; Remy and Remy, 1978). Some seed ferns (e.g., *Peltaspermum* Harris, 1937) and putative cycadophyte-like leaves were described from the Lopingian of the Southern Alps (Poort and Kerp, 1990; Krainer, 2000).

The discovery of a new fossiliferous horizon, rich in megafossils with well-preserved cuticles, in Bletterbach gorge, is relevant because it is the first Lopingian macroflora of the Southern Alps with several taxa of putative horsetails, seed ferns and *Taeniopteris*. These groups are usually minor representatives in Lopingian floras. Although fragments are small, the preservation is good; in most cases they yield good cuticles. The here described fossils show the diversity of sphenophyte, seed fern and cycad-like foliage from Lopingian strata of the Southern Alps.

2. Material and methods

Bletterbach gorge is located at the western margin of the Dolomites, between the villages Aldein/Aldino and Radein/Redagno (for details see Kustatscher et al., 2012). The basal rocks of the gorge are andesites, and extrusive and ignimbritic rhyolites of the Auer/Ora Formation of the Athesian Volcanic Group (formerly Bozen Quartzporphyry). The top of this succession has been dated to 274.1 ± 1.4 Ma, i.e., Kungurian, late Cisuralian (Avanzini et al., 2007; Marocchi et al., 2008). The overlying Gröden Sandstone is characterized by alternations of reddish–greyish fluvial siliciclastics, evaporites and mixed carbonate–siliciclastics (Italian IGCP-203 Group, 1986; Massari et al., 1988; Ori, 1988; Massari et al., 1994) of Wuchiapingian (early-middle Lopingian) age (Kustatscher et al., 2012). About 80 m from the base of the succession is the cephalopod bed (formerly often referred to as Cephalopoden-Horizont/Cephalopod Horizon), a 2 m thick marine limestone containing a sparse cephalopod fauna (Italian IGCP-203 Group, 1986; Massari et al., 1988, 1994). Immediately above the cephalopod bed is a bed very rich in dispersed cuticles from which several taxa were described (Clement-Westerhof, 1984, 1986, 1987; Poort and Kerp, 1990). This bed is further referred to as the cuticle bed.

About 500 plant megafossils have been discovered in a fossiliferous bed of the Gröden Sandstone, c. 1 m below the cephalopod bed. This material is stored at the Museum of Nature South Tyrol (NMS) in Bozen/Bolzano (collection numbers with the prefix "PAL"). Twenty-eight fragments of horsetails, seed ferns and putative cycads were identified. In addition, 45 specimens collected in the 1970s and 1980s by staff of Utrecht University (Jopie A. Clement-Westerhof, Henk Visscher, Hans Kerp and others) were examined (prefix "UU"). For comparative purposes some unpublished megafossils from other Permian deposits in the Southern Alps, stored at Utrecht University, are also discussed in this paper.

The material was studied with a dissecting stereomicroscope. Cuticles were prepared by maceration in Schulze's reagent (30% HNO_3 and few grains of $KClO_3$), subsequently treated with 10% KOH and rinsed with distilled water, then mounted in glycerine jelly on slides for light microscopic analyses and finally sealed with paraplast (Kerp, 1990; Kerp and Krings, 1999). Bulk macerations were performed in order to obtain better preserved cuticles of the various taxa. Samples were treated with HF (47%) for several days, sieved and then processed using the same procedure as for the in situ material. Hand specimens were photographed with a Canon Eos D550 digital camera, according to procedures outlined by Kerp and Bomfleur (2011). Cuticles were analysed with a Leitz Diaplan microscope and photographed with a Nikon DS-5Mc/Nikon DS-L2 digital camera.

3. Systematic palaeontology

3.1. Sphenopsids

Several horsetail fossils were found in the new flora and in the collection of Utrecht University. The dispersed hexagonal sporophyll heads that are 4–6 mm in diameter (PAL1395, Plate I, 1) may be referable to *Equisetites* Sternberg 1833. A stem fragment (33 mm long, 18 mm wide) shows 2 mm broad ribs (UU 23788), but nodes cannot be observed. Putative fragments of leaf sheaths (45–68 mm long, 21–38 mm wide) have three to six pointed, 11–14 mm long and 9–12 mm wide 'teeth' (PAL1377, 1427/1428, Plate I, 2).

3.2. Pteridosperms

Order Peltaspermales Němejc 1968
Family Peltaspermaceae Thomas ex Harris 1937

Germaropteris Kustatscher, Kerp et Van Konijnenburg-van Cittert gen. nov.
Type: Germaropteris martinsii (Germar in Kurtze 1839) Kustatscher, Kerp et Van Konijnenburg-van Cittert comb. nov.
Etymology: The genus is named after Ernst Friedrich Germar (1786–1853), mineralogist and entomologist, professor for mineralogy and museum director in Halle (Saale), author of several palaeobotanical studies, e.g., on Zechstein floras (Germar in Kurtze, 1839; Germar, 1840) and Carboniferous (Pennsylvanian) floras (Germar and Kaulfuss, 1831; Germar, 1844–1853). Germar first described the type species of the new genus established here.

Diagnosis: Small to medium-sized bipinnate, rarely pinnate or tripinnate fronds. Fronds overtopping in the apical portion, in some cases with double apical (pseudo-)dichotomies in larger, (partially) tripinnate fronds. Pinnae subopposite to alternate. Primary rachis with intercalary pinnules. Pinnules small, semi-circular, linguiform to elongate linguiform, broadly attached, decurrent to basally fused in the basal and apical frond portions and pinna apices, entire-margined, crenulate to pinnatifid. Pinnules thick and fleshy with rounded apices and a pinnate venation that is usually hidden by the thick cuticle. Leaves amphistomatic, stomata irregularly scattered; stomatal complexes sunken, monocyclic with 4–8 (usually 5–6) subsidiary cells; papillae may be present. Ovuliferous organs consisting of peltate discs with a central stalk and marginal lobes; upper surface with radiating ribs.

Discussion: Germaropteris is monotypic but the type species has a long and complex taxonomic history. Foliage and ovuliferous organs were first described by Germar (in Kurtze, 1839) and Göppert (1850) respectively, but under different names. Foliage and ovuliferous organs were linked by Poort and Kerp (1990). The foliage is common in Lopingian strata of Europe and has also been reported from China (Poort and Kerp, 1990). The foliage has been assigned to various genera, e.g., *Alethopteris* Sternberg 1825 (Germar in Kurtze, 1839; Althaus, 1846; Geinitz, 1862), *Callipteris* (e.g., Zeiller, 1906; Gothan and Nagalhard, 1921; Stoneley, 1958; Schweitzer, 1962; Barthel and Haubold, 1980), *Lepidopteris* (Townrow, 1960) and, more recently, *Peltaspermum* (Poort and Kerp, 1990). The name *Callipteris martinsii* (Germar in Kurtze 1839) Zeiller, 1906 has been used most frequently. However, *Callipteris* Brongniart 1849 is a later homonym of *Callipteris* Bory 1804 and, therefore, illegitimate (Kerp, 1981, 1986). Townrow (1960) transferred the species to *Lepidopteris* (Peltaspermales), because of similarities in overall frond morphology including the presence of intercalary pinnules and subepidermal swellings (“blisters”), and the morphology of the stomatal apparatuses. *Lepidopteris* was established by Schimper (1869); Harris (1932) designated *L. stuttgardiensis* (Jaeger 1827) Schimper, 1869 as the lectotype of the genus. Peltaspermaceae was introduced by Thomas (1933) to include the foliage and seed-bearing organs described as *Lepidopteris natalensis* Thomas 1933.[2] With the description of the name-giving genus *Peltaspermum* and type *P. rotula* Harris 1937, Harris (1937) validated the family. The ovuliferous organ *Peltaspermum rotula* from the Rhaetian of East Greenland was correlated with the foliage *Lepidopteris ottonis* (Göppert 1836) Schimper, 1869 and the pollen organ *Antevsia zeilleri* Harris 1937, based on similarities in epidermal anatomy and repeated co-occurrences (Harris, 1937). Unfortunately, the type species of *Lepidopteris*, *Lepidopteris stuttgardiensis*, is rather incompletely known. Larger specimens were found but cuticle and reproductive organs are still unknown. Initially, peltasperms were considered exclusively Mesozoic. In the late 1970s and early 1980s it became clear that this group had a range extending from the Lopingian (Gomankov and Meyen, 1979; Meyen and Gomankov, 1980) or even Cisuralian (Kerp, 1982).

When *Peltaspermum*-type ovuliferous organs were correlated with *Lepidopteris* (al. *Callipteris*) *martinsii* foliage, based on similarities in epidermal anatomy and consistent co-occurrences, Poort and Kerp (1990) emended the diagnosis of *Peltaspermum*, a genus originally defined for peltate ovuliferous organs, to include both foliage and ovuliferous organs. They argued that the combination of characters of all known parts and organs of a fossil plant that belong together should define a genus and stated that the genus should be named after the ovuliferous organs being the most typical part of the seed plant. However, this latter principle for naming fossil plants was not formally accepted until recently (McNeill et al., 2012). Although the combination *Peltaspermum martinsii* has been used by several authors (e.g., Retallack, 2001; Uhl et al., 2012; Uhl, 2013), others preferred to apply the name *L. martinsii* (e.g., Karasev and Krassilov, 2007; Kustatscher et al., 2012; Zhang et al., 2012; Karasev, 2013). An additional complication is that plants with different types of foliage appear to have had the same type of peltasperm ovuliferous organ, i.e., *Lepidopteris* and *Scytophyllum* Bornemann 1856 (e.g., Dobruskina, 1969; Schweitzer and Kirchner, 1998; Kustatscher et al., 2007; Kustatscher and Van Konijnenburg-van Cittert, 2010). Bilaterally symmetrical ovuliferous organs of the *Autunia* type also apparently belonged to different types of foliage, i.e., callipterids (Kerp, 1982, 1988), *Supaia* (Wang, 1997) and *Lepidopteris* (Thomas, 1933; Anderson and Anderson, 2003).

Naugolnykh (2001, 2007) suggested excluding forms with bilaterally symmetrical ovuliferous organs from the peltasperms, based on the assertion that radially and bilaterally symmetrical ovuliferous organs represent independently developed lineages. According to Karasev (2009) this would be supported by similar bilaterally symmetrical ovuliferous organs from the Upper Triassic of South Africa, where they were found in organic connection with leaves of *Sphenobaiera* Florin 1936 (Anderson and Anderson, 2003). However, it must be noted that *Autunia*-type ovuliferous organs have been recorded in association with callipterid foliage in more than just a few localities; in most of these ginkgophyte foliage is absent. Moreover, a specimen from the Transition Zone (Sakmarian, Cisuralian) of Lodève (southern France) shows organic connection between foliage of *Autunia conferta* (Sternberg 1826) Kerp 1988 and bilaterally symmetrical ovuliferous organs (Galtier and Broutin, 1995). The position on the stem suggests that the *Autunia* seed-bearing structure is homologous to a frond.

Many genera have been attributed to peltasperms in recent decades. Some on the basis of foliar morphology, several on the basis of foliar and cuticular morphology, others exclusively on the basis of cuticular morphology, some on the basis of the morphology of the ovuliferous organs, and relatively few on the basis of the combination of foliar and cuticular morphology and reproductive organs. Since the 1980s peltasperms and presumed peltasperms have been reported from Permian deposits in various parts of Europe and North Africa (Meyen, 1982, 1984; Gomankov and Meyen, 1986; Kerp, 1988; Poort and Kerp, 1990; Naugolnykh and Kerp, 1996; Kerp et al., 2001; Naugolnykh, 2001; Karasev, 2007; Karasev and Krassilov, 2007; Karasev, 2009, 2013), from China (Wang and Wang, 1986; Wang, 1997; Liu and Yao, 2000; Wang, 2010), and North America (DiMichele et al., 2005; Krings et al., 2005a,b; Chaney et al., 2009). Even though the natural affinities need to be further tested and relationships between individual taxa have to be further resolved, it is clear that peltasperms were probably more common and more diverse during the Permian than in the Mesozoic.

The material from the Bletterbach locality belongs to one of the few species for which foliage and ovuliferous organs are known, both with cuticle. Linkage was based on their co-occurrence in the Bletterbach locality and in the German Zechstein, and on similarities in epidermal anatomy (Poort and Kerp, 1990). Uhl (2013) recently described anatomical details of the foliage. For reasons given above the species can no longer be assigned to *Peltaspermum*. Attribution to *Lepidopteris* is not realistic either. *Lepidopteris* has been defined as a frond with pecopteroid pinnules with pinnate venation. The most complete fronds are known from *Lepidopteris ottonis*, *Lepidopteris stormbergensis* (Seward 1903) Townrow, 1956 and *Lepidopteris toretziensis* Stanislavky 1976 (Harris, 1937; Townrow, 1956, 1960; Stanislavsky, 1976; Anderson and Anderson, 1989). These latter species have very regular monopodial fronds with an acute frond apex and acute pinna apices. Except for the type species, all *Lepidopteris* species have slightly triangular, entire-margined pinnules with a clear pinnate venation. In contrast, the species under consideration has rather irregular, in some cases bifurcated, commonly apically overtopping fronds. The apical part of the frond rachis shows a more or less clear zig-zag course with a number of successive, unequally developed false dichotomies in which the longer branches that dichotomize again alternate with shorter unbranched ones. Pinnules near the frond and pinna apices are commonly enlarged and do not gradually become smaller as in *Lepidopteris*. Pinnules are small, symmetrical, semi-circular to slightly lobed in larger ones and sporadically pinnatifid. The venation is pinnate but always obscured by the thick cuticle in hand specimens and only becomes visible after incomplete maceration. Fronds are rather small and plump with thick fleshy pinnules unlike the much larger, slender fronds of *Lepidopteris* that bear much thinner pinnules. In our opinion these differences justify

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[2] The name *Lepidopteris natalensis* (foliage) is now regarded as a synonym of *L. stormbergensis* (Seward 1903) Townrow 1956.

the establishment of a new genus to satisfactorily accommodate one of the first described peltasperms.

Germaropteris martinsii (Germar in Kurtze 1839) Kustatscher, Kerp et Van Konijnenburg-van Cittert comb. nov.
Plate I, 3–6; Plate IV, 1; Fig. 1.

Basionym: Alethopteris martinsii (Germar in Kurtze 1839), Commentatio de petrefactis quae schisto bituminoso mansfeldensi repriuntur, pp. 34–35.
Holotype: The specimen figured by Germar in Kurtze (1839, pl. III, 2).
Emended diagnosis: For the emended diagnosis and a more detailed synonymy refer to Poort and Kerp (1990, pp. 206–207).

Foliage — selected synonymy

1839	*Alethopteris martinsii* Germar in Kurtze, pp. 34, 35, 38, pl. III, 2.
1840	*Alethopteris martinsii* Germar, pp. 35–36.
1846	*Alethopteris martinsii* Althaus, pl. 1, 3.
1846	*Caulerpites crenulatus* Althaus, pl. I, 4.
1848	*Pecopteris* (*Alethopteris*) *martinsii* Geinitz, p. 20.
1862	*Alethopteris goepperti* Geinitz, p. 142, pl. XXV1, 7, 8.
1906	*Callipteris martinsii* Zeiller, p.71.
1907	*Callipteris martinsi* Gothan pp. 1–4, figs. 1, 2.
1921	*Callipteris martinsi* Gothan and Nagalhard, pp. 451–453, pl. 6, 5, 6, pl. 7, 13.
1928	*Callipteris martinsi* Weigelt, pp. 457, 458, pl. II, 14, 15, 26; pl. VII, 1–14, pl. 3, 7, 14, (22?).
1958	*Callipteris martinsi* Stoneley, pp. 313–315, figs. 5, 6, pl. 37, 2, 5.
1960	*Lepidopteris martinsii* Townrow, pp. 345–347, figs. IL, 2J, 3G–K, 4A, B, 5J, 6D.
1962	*Callipteris martinsi* Schweitzer, pp. 339–340, fig. 4, pl. 1, 3, 4, pl. 3, I.
1990	*Peltaspermum martinsii* Poort and Kerp (*per partem*), pp. 203, 206–208, 210, 214, 216, pl. I–V, pl. VI, 1 (*per partem*).
2012	*Lepidopteris martinsii*, Kustatscher et al., p. 4, pl. I, 7.

Ovuliferous organs — selected synonymy

1850	*UIlmannia bronni* Göppert, p. 188, pl. 20, (?21, 22), 24–26.
1864–65	*Ullmannia bronni* Göppert, pp. 226, 227, pl. 45, 21 23, 25.
1884	*Strobilites bronnii* Solms–Laubach, pp. 19–24, pl. II, 2–9, 16–19.
1944	*Strobilites bronnii* Florin, p. 447, pl. 169–170, 5–9, 13–2.
1958	*Strobilites bronni* Stoneley, p. 329, pl. 40, 7–11.
1990	*Peltaspermum martinsii* Poort and Kerp, pp. 207, 216–218, pl. VI, 1 (parte), 2–7, pl. VII, VIII.
2012	*Peltaspermum* sp. Kustatscher et al., p. 4, pl. I, 3.

Description of the foliage: Two small macroscopic fragments were found in the new Bletterbach locality (PAL1017, 1033, pl. I, 3). The pinna fragments are up to 20 mm long and 7 mm wide. Pinnules (3.5–4 mm long and 2 mm wide) arise from the 1 mm wide rachis (PAL1017, pl. I, 3). Two additional specimens are kept in the Utrecht collection (UU cut. 1246, UU 23776). The most complete frond fragment is 30 mm long and consists of a 2 mm wide rachis that is densely covered by large blister-like swellings. The frond rachis bears fragments of at least five, up to 8 mm long pinnae with densely positioned, 1.5–2 mm long and 1–2 mm wide pinnules with a rounded apex (UU cut. 1246, pl. I, 4); venation cannot be observed.

The fronds are amphistomatic with a thinner cuticle with more stomata on the lower surface. The epidermis is characterized by

Plate I. Scale bar = 1 cm.

1. ?*Equisetites* sp., sporophyll head (NMS PAL 1395)
2. Fragment of equisetoid leaf sheath (NMS PAL 1428)
3. *Germaropteris martinsii* (Germar in Kurtze) comb. nov., pinnae fragment (NMS PAL 1017)
4. *Germaropteris martinsii*, frond fragment (UU cut. 1246)
5. *Germaropteris martinsii*, *Peltaspermum*-type ovuliferous disc (NMS PAL 1036)
6. *Germaropteris martinsii*, *Peltaspermum*-type ovuliferous disc (NMS PAL 978)
7. *Sphenopteris suessii*, frond fragment (NMS PAL 1412)
8. *Sphenopteris suessii*, frond fragment (NMS PAL 1409)
9. *Sphenopteris suessii*, pinnae fragments (NMS PAL 1408).

Plate II. Scale bar = 1 cm. (see on page 70)

1. *Sphenopteris* sp., frond fragment (NMS PAL 1478)
2. Pinna with alethopteroid pinnules, pinnules attached to the rachis with decurrent proximal basis (UU 23763)
3. Pinna with alethopteroid pinnules, most complete frond fragment (UU 23773)
4. Pinna with alethopteroid pinnules, pinnules connected with a wing along the rachis (UU 23779)
5. Pinna with alethopteroid pinnules, slightly falcate pinnules with a rounded apex (UU 23761).

Plate III. Scale bar = 1 cm. (see on page 71)

1. *Taeniopteris* sp. A, most complete specimen (NMS PAL870)
2. *Taeniopteris* sp. B, most complete specimen (NMS PAL 844)
3. *Taeniopteris* sp. B, specimen that yielded the best cuticles (UU 23786)
4. *Taeniopteris* sp. A, frond fragment with clear venation (NMS PAL 830)
5. *Taeniopteris* sp. B, frond fragment with clear venation (UU 23764)
6. Fragment of a cycad-like leaf?, apical leaf fragment, (NMS PAL 1003).

Plate IV. Scale bar = 50 μm. (see on page 72)

1. *Germaropteris martinsii*, cuticle with stomata covered by papillae (NMS PAL 1017)
2. *Sphenopteris suessii* Geinitz 1869, cuticle with isodiametric epidermal cells (NMS PAL 1412)
3. *Sphenopteris suessii*, stomata surrounded by five subsidiary cells (NMS PAL 1409)
4. *Sphenopteris* sp., cuticle with alternations of stripes of isodiametric epidermal cells devoid of stomata (indicating veins?) and rows of stomata immersed in lightly smaller epidermal cells (NMS PAL 1478)
5. *Sphenopteris suessii*, stomata surrounded by five subsidiary cells (NMS PAL 1409)
6. Alethopteroid pinnule, cuticle with stomata are arranged in short rows (UU 23773)
7. *Sphenopteris* sp., stomata surrounded by a ring of 5–8 subsidiary cells (NMS PAL 1478)
8. Alethopteroid pinnule, stomata with 5–6 subsidiary cells, general epidermal cells show the base of trichomes, detail of Plate IV, 6 (UU 23773).


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Plate II (*caption on page 68*).

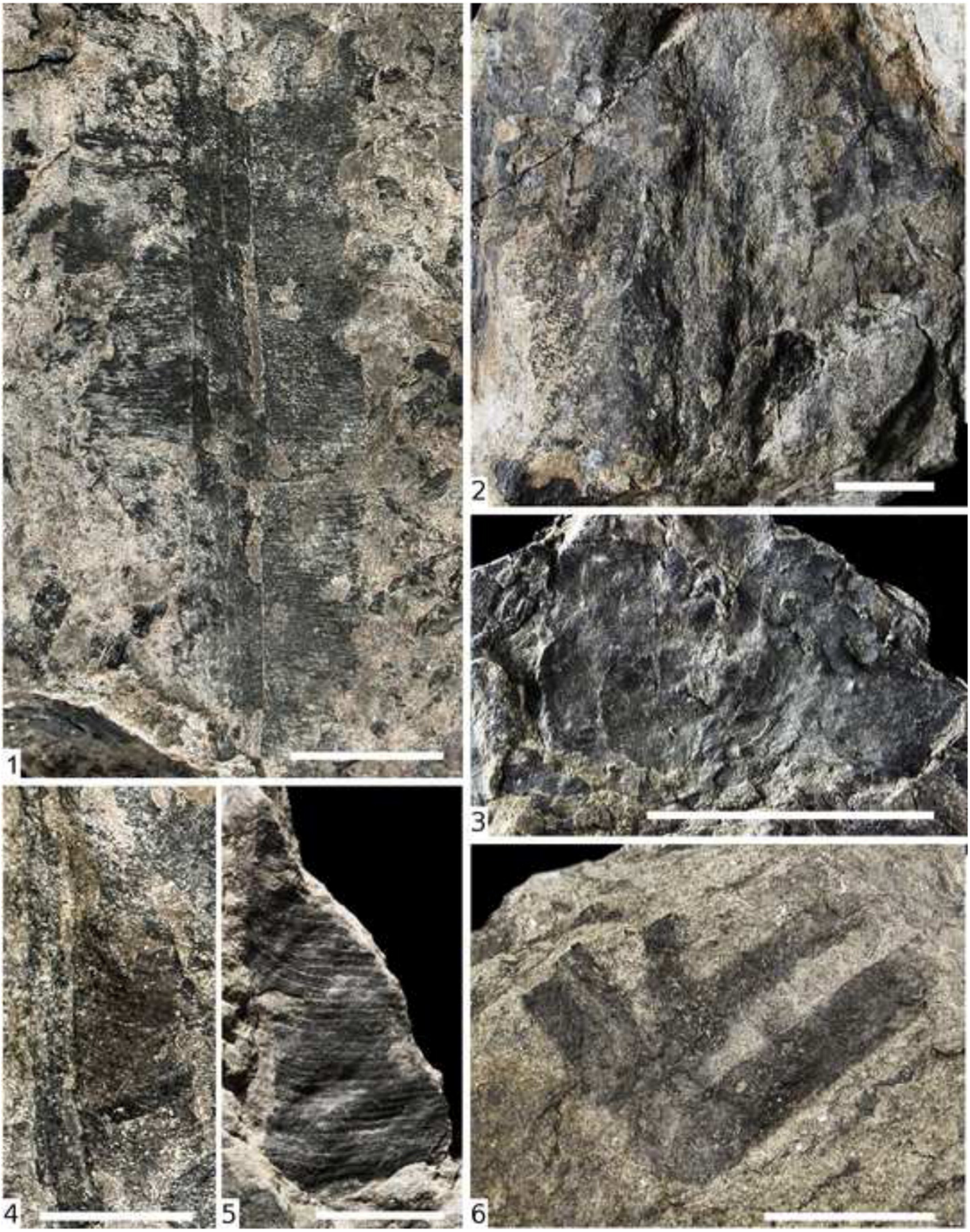

Plate III (*caption on page 68*).

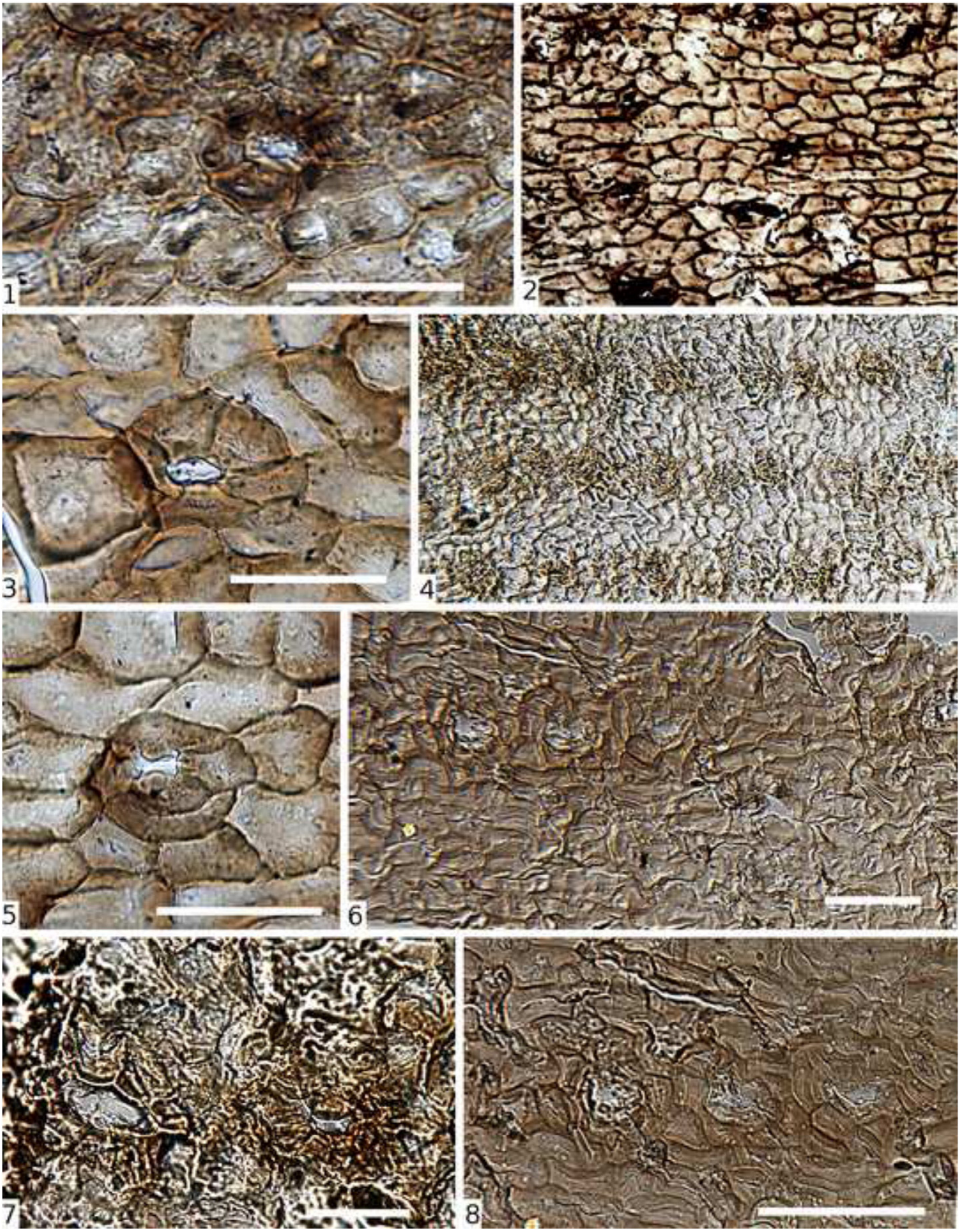

Plate IV (*caption on page 68*).

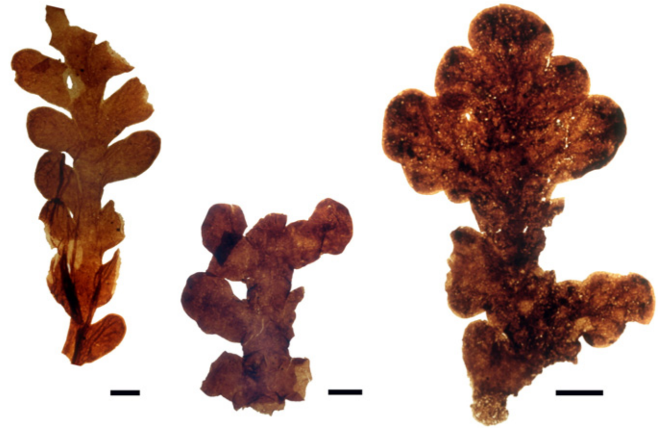

Fig. 1. Incompletely macerated pinnae fragments of *Germaropteris martinsii* (Germar in Kurtze) comb. nov. showing the venation pattern (dispersed cuticles stored at Münster University). Scale bar = 1 mm.

polygonal isodiametric cells bearing papillae. The epidermal cells are smaller on the upper (20–26 μm) than on the lower surface (25–35 μm). The stomata are irregularly scattered and sunken. The stomatal pit is protected by the overarching papillae of the 5–6 (rarely 7 or 8) subsidiary cells (PAL1017, pl. IV, 1). Stomatal complexes never share subsidiary cells but can be closely spaced, especially on the lower side of the pinnule surface. The subsidiary cells are smaller (15–22 μm) than the normal epidermal cells and trapezoid to polygonal in shape.

Description of the ovuliferous discs: Only one well-preserved specimen (PAL978, 1036: part and counterpart) of a *Peltaspermum*-type ovuliferous disc has been found so far. The radially symmetrical, peltate ovuliferous disc of 21 mm diameter is divided into 14 lobes. The lobes are deeply incised, 7–8 mm long and 2.5 mm wide, with a rounded apex (PAL978, 1036, Plate I, 5–6). One more specimen (PAL1468), 21 mm in diameter, might belong to this species, but its preservation is insufficient for confident identification. The new specimens from the Bletterbach did not yield any cuticle.

Foliage: NMS PAL1017, 1033, UU cut. 1246, UU 23776.
Ovuliferous organs: NMS PAL978, 1036, ?PAL1468.

Remarks: Unfortunately, only two small, macroscopically identifiable remains were found. The intercalary pinnules typical for the species are not visible in the material from the new locality. Nonetheless, dimensions and shape of the pinnules and the cuticle characters allow attribution to *Germaropteris martinsii*. Two additional, poorly preserved fragments from Ortisei (Ronca, Italy, Lopingian) and one specimen from the Collio Formation (late Artinskian–Kungurian) are stored in the collection of Utrecht University. Although only few macroscopically recognizable specimens were found, the species is not rare in bulk macerations, in which it is the most common form after the conifers (Poort and Kerp, 1990). *Germaropteris martinsii* cuticles are easily recognizable by the shape and distribution of the stomata. In the Bletterbach locality most *G. martinsii* cuticles are strongly papillate, although the size and density of papillae vary within a single sample (Poort and Kerp, 1990). The occurrence of papillae is not a diagnostic character. In *G. martinsii* from the German Zechstein, papillae are usually restricted to the subsidiary cells, whereas normal epidermal cells are non-papillate or have only slight thickenings; papillae may be completely absent in specimens from northern England (Stoneley, 1958). Poort and Kerp (1990, pl. 2, 5; fig. 2) illustrated a pinna fragment from Bletterbach. The incompletely macerated cuticle of the leaf fragment shows the pinnate venation (Fig. 1). Venation is not visible in untreated remains, because pinnules have very robust cuticles and they were very thick and fleshy; the cuticle and the remaining coaly material (mesophyll) obscure the venation pattern.

Three-dimensionally preserved peltate ovuliferous discs were originally described as *Ullmannia bronnii* Göppert, 1850 and interpreted as cross-sections of male conifer cones (Göppert, 1850, 1864–65). Solms-Laubach (1884) introduced the name *Strobilites bronnii*, which was also applied by Florin (1944) and Stoneley (1958) for material from Germany and England. None of these authors questioned the coniferous nature of these structures, until morphologically identical specimens with very prominent marginal lobes as in several of the three-dimensionally preserved and compression specimens were found in cuticular preservation (Poort and Kerp, 1990). The cuticles were not conifer- but peltasperm-like and all were found associated with peltasperm foliage here assigned to *Germaropteris martinsii*. Some of the discs illustrated by the above authors are smaller and have fewer lobes. However, it should be noted that within a single locality a considerable variability may occur, e.g., in Adorf (NE Hesse, Germany) from where more than a dozen discs are known. The marginal lobes are more prominent in some specimens than in others. They are largely overlain by the disc itself in many compression specimens and, therefore, barely visible. Lobes seem to be exceptionally well developed in some compressions, but this may partly be a preservational feature. The lamina between the ribs apparently disappears first, leaving the prominent ribs behind when discs start to decay. Such partly decayed specimens may suggest that discs were deeply incised.

Distribution: *Germaropteris martinsii* is one of the most common pteridosperms in the Lopingian of Eurasia. It has been recorded from England (Stoneley, 1958) and Germany (e.g., Kurtze, 1839; Germar, 1840; Geinitz, 1862; Schweitzer, 1962; Poort and Kerp, 1990) and from the Permian of China (see Poort and Kerp, 1990).

Pteridosperms incertae sedis
Sphenopteris (Brongniart 1822) Sternberg 1825
Sphenopteris suessii Geinitz, 1869
Plate I, 7–9; Plate IV, 2, 3, 5

Selected synonymy

1869	*Sphenopteris suessii*, Geinitz, pp. 459–60. pl. 5, 3–7
1896	*Sphenopteris suessii*, Sordelli, p. 10, pl. 1, 1
1977	*Sphenopteris suessii*, Remy and Remy, p. 202, fig. 88
1978	*Sphenopteris suessii*, Remy and Remy, p. 58, pl. 7, 1–3
2001	*Sphenopteris suessii*, Visscher et al., p. 117, pl. 1, 6–7.

Description: The pinna fragments are up to 43 mm long and 23 mm wide with a 1.5–2.5 mm wide rachis (e.g., PAL1412, Plate I, 7). The pinnules are attached (sub)oppositely to oppositely to the rachis. They are inversely lanceolate and up to 13 mm long and 9 mm wide (e.g., PAL1408, 1409, Plate I, 8–9). Pinnule bases are constricted.

The leaves are amphistomatic. The epidermal cells are isodiametric but irregular rows of elongate epidermal cells also occur (probably indicating veins). The isodiametric epidermal cells of the upper pinnule surface (22–30 μm, mean 28 μm in diameter) are smaller than those of the lower surface (30–50 μm, mean 38 μm in diameter). The elongate epidermal cells are about 35–60 μm long (mean 47 μm) and 12–20 μm wide (mean 17 μm). Some epidermal cells are covered by small papillae (e.g., PAL1412, Plate IV, 2). The stomata are scattered irregularly in (?intercostal) fields with isodiametric cells. The slightly sunken thin-walled guard cells are encircled by 4–5 subsidiary cells (e.g., PAL1409, Plate IV, 3, 5); the two polar cells are isodiametric to slightly elongate (15–30 μm), the two (or in some cases three) lateral cells are more or less butterfly-shaped to trapezoid (15–25 × 25–40 μm). The periclinal and anticlinal walls of the subsidiary cells are thicker than those of the normal epidermal cells. Some lateral cells bear papillae extending partially over the stomatal pit (Plate IV, 5).

Material: NMS PAL1408, 1409, 1412.

Remarks: The material is attributed to *Sphenopteris suessii* based on the general morphology of the leaves, especially the constricted basal pinnules. This is the first time that the cuticle of this species is described.

Two more fragments (UU 23807, 23808) were found in Cortiana and Ulbe near Schio in the Vicentinian Alps (collection Utrecht University). These specimens are better preserved than those from Bletterbach. The fragments are up to 70 mm long and 50 mm wide, with a 1–1.2 mm thick rachis and 13–18.5 mm long and 7.5–9 mm wide pinnae. The pinnae have a less than 1 mm thick rachis and elongated pinnules. The (sub)alternately inserted pinnules are inverse lanceolate with the broadest part at the apex. The basal pinnules divide again pinnately (UU 23807).

Comparisons: Pinnules of *Sphenopteris patens* (Althaus) Geinitz 1848 are undivided or dissected only once; basal pinnules of *Sphenopteris suessii* are constricted. Pinnules of *Sphenopteris kukukiana* Gothan et Nagalhard 1921 are linear with a truncate apex. The obovate pinnules of *Sphenopteris geinitzii* Göppert 1864–65 are markedly imbricate; those of *Sphenopteris bipinnata* (Münster) Geinitz 1848 dentate, whereas they are markedly clavate with divided basal pinnules in *Sphenopteris dichotoma* Althaus, 1846.

Distribution: The species seems to be restricted to the Permian of the Alps. It was recorded originally from the Collio Formation (Artinskian–Kungurian) in the Trompia Valley (e.g., Geinitz, 1869; Sordelli, 1896) and has now also been found in Lopingian strata of Cortiana (near Schio) and Ulbe (Recoaro area) and Bletterbach.

Sphenopteris sp.
Plate II, 1; Plate IV, 4, 7

Description: A single specimen is identified as *Sphenopteris* sp. (PAL1478, pl. II, 1). The pinna fragment is 36 mm long and 17 mm wide. Pinnules are attached (sub)alternately to a 3 mm wide, striate rachis, at a distance of 10 mm; only two pairs are present. The pinnules are more or less irregularly dichotomous and 11 mm long. They fork at least twice in the proximal part. The segments are free, 5 mm long and 1.2 mm wide. The venation is unclear.

The leaves are amphistomatic with a thin cuticle. The epidermal cells are isodiametric (25–35 μm, mean 30 μm). The cuticle is divided in alternations of stripes of 4–5 isodiametric epidermal cells devoid of stomata (veins?) and rows of stomata immersed in slightly smaller, isodiametric epidermal cells (PAL1478, pl. IV, 4). The stomatal apparatuses are monocyclic, consisting of two thin-walled, deeply sunken guard cells surrounded by a ring of 5–8 subsidiary cells. The subsidiary cells are isodiametric to almost circular, smaller than the normal epidermal cells (10–28 μm, mean 15 μm), and protected by thick papillae (PAL1478, pl. IV, 7).

Material: NMS PAL1478

Comparisons: This specimen differs from *Sphenopteris suessii* mostly in the shape of the basal pinnules (irregular dichotomized in *Sphenopteris* sp., contracted in *S. suessii*) and the stomatal complexes. The stomata of *Sphenopteris* sp. are arranged in distinct, darker rows and surrounded by 5–7 stronger cutinized subsidiary cells with papillae overarching the stomatal pores, whereas *S. suessii* has two polar and 2–3 lateral subsidiary cells being weaker cutinized than the normal epidermal cells. The specimen also resembles *Sphenopteris patens*, *Sphenopteris kukukiana* and *Sphenopteris gillitzeri* Weigelt, 1931 from the Kupferschiefer, lower Zechstein (Wuchiapingian) of Germany (Gothan and Nagalhard, 1921; Weigelt, 1931) in having linear to wedge-shaped pinnules; in our new specimen they are flabellate and not pinnately arranged. Our specimen differs from *Sphenopteris bipinnata* from the Kupferschiefer of Germany in having elliptical pinnules with an entire to slightly crenate margin. The pinnules in *Sphenopteris geinitzii* from the Kupferschiefer of Germany are more closely inserted, imbricated, and broadly elliptical. Pinnules of *Sphenopteris dichotoma* from the Zechstein of Germany and England are elliptical to wedge-shaped and basal, larger pinnules are commonly divided into three segments (Althaus, 1846; Schweitzer, 1960).

Pinnae with alethopteroid pinnules
Plate II, 2–5, IV, 6, 8

Description: The small frond fragments are up to 50 mm long and 26 mm wide (e.g., UU 23761, 23773, Plate II, 3, 5). Pinnules arise (sub)alternately, at c. 45° from the 1–2 mm wide rachis (e.g., UU 23773, Plate II, 3). Pinnules are oblong to slightly falcate with a rounded apex and a decurrent proximal base (e.g., UU 23779, Plate II, 4). The pinnule margins never touch; generally the pinnules are separated by few millimetres but adjacent pinnules are connected by a wing along the rachis (e.g., UU 23779, Plate II, 4). The 5–15 mm long and 5–5.5 mm wide pinnules have a distinct midrib. The midrib arises acutely from the rachis on the acroscopic side of the pinnule base, curves and runs to about 1/2 to 2/3rd of the pinnule length. The secondary veins are distinct, arise at an angle of 45–65° and divide once in the distal half of the lamina (UU 23763, 23779, Plate II, 2, 4); very rarely they also fork near the midvein.

Only one small cuticle fragment was obtained (Plate IV, 6, 8). The irregularly arranged epidermal cells are isodiametric (16–28 μm, mean 21 μm) to rectangular (23–55 × 10–25 μm). Some bear papillae while trichomes are common; the latter, typically borne by isodiametric cells, have a base of 11–18 μm (mean 14 μm) in diameter. Stomata are arranged in rows, they are closely spaced but never share subsidiary cells. The guard cells are slightly sunken, surrounded by 5 (rarely 4 or 6) subsidiary cells bearing small papillae. The subsidiary cells (13–21 μm, mean 16 μm) are smaller than normal isodiametric epidermal cells.

Material: NMS PAL844, 990; UU 23761, 23762, 23763, 23773, 23779, 23796, 23798, 23800.

Remarks: The pinna fragments are very small, hampering a generic assignment. Considering the pinnule shape with its decurrent base, the entire pinnule margin and the distinct alethopterid venation, this material might be assigned to *Alethopteris* or it might be a callipterid with alethopteroid pinnules. However, the last occurrence of *Alethopteris* is in Cisuralian strata of China (Wang, 2010), although Hu (1980) reported ?*Alethopteris huiana* Lee 1964 from the lower Cangfanggou Group (Lopingian) in northern Xinjiang, China. The youngest alethopterid from the European Permian is *Alethopteris schneideri* Sterzel 1881 from the Rotliegend (Asselian–Sakmarian, Cisuralian) of Saxony and Thuringia (Germany), a species described in great detail by Barthel (1976, 2006). According to the latter author, *A. schneideri* shows considerable variation and our material would fall within the natural variation outlined by Barthel (1976, 2006). Another form from the Rotliegend formerly assigned to *Alethopteris*, *Alethopteris subelegans* (Potonié 1893) Franke 1913, is according to Barthel (1981) a fern (*Scolecopteris pseudobucklandii* (Andrä in Germar 1853) Stur 1883). Forms from Lopingian strata previously described as *Alethopteris*, i.e., *Alethopteris martinsii* and *Alethopteris goeppertii*, are now accommodated in *Germaropteris martinsii*.

Apart from *Alethopteris*, several other taxa have alethopteroid pinnules, notably callipterids. Most have their last occurrence in the Cisuralian–Guadalupian. However, one form – *“Callipteris” bexelii* Durante, 1992[3] – has been reported from the Lopingian strata exposed

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[3] The generic name *Callipteris* is placed between quotation marks, because the generic name *Callipteris* Brongniart 1849 is illegitimate. This species has not yet been transferred to another genus of callipterid foliage.

in the Dashankou Section, Yumen, Nanshan region, Gansu, NE China (Durante, 1992). This locally very abundant species, which occurs in a flora with Angaran affinities, has alethopteroid pinnules that are quite similar to those of *Autunia conferta* in having linguiform decurrent pinnules with a clear, slightly sunken midvein and rather straight, densely spaced lateral veins. However, the two species strongly differ in their cuticular structure (Wang and Kerp, in prep.). Specimens of *"C." bexelii* with shorter pinnules are very similar to the pinnae with alethopteroid pinnules from Bletterbach.

It will be very difficult to resolve the real affinity of the fragmentary material at hand. However, a pteridosperm affinity is evidenced by its thick cuticle. The presence of this type of foliage is remarkable, because such forms have not previously been found in Lopingian strata of Europe.

Distribution: This taxon is found in the newly discovered fossiliferous bed below the cephalopod bed and in the cuticle horizon immediately overlying the cephalopod bed.

3.3. Taeniopterids

Taeniopteris Brongniart 1828

Remark: Taeniopteris is a genus for fossil linear-lanceolate, entire-margined leaves with a well-developed midvein and numerous straight, sometimes unforked but commonly once to several times forked, parallel lateral veins reaching the lateral margins at angles of 70–90°. This type of foliage is known from various groups of plants including ferns, pteridosperms, Pentoxylales, cycads and bennettitaleans (Taylor et al., 2009). Representatives are known from the Stephanian (Upper Pennsylvanian) to the Cretaceous. Several species originally included in this very heterogeneous genus have later been assigned to other genera, mostly based on cuticular characters. One species that is widespread in the Lopingian of Europe was transferred to *Lesleya* Lesquereux 1880, i.e., *Lesleya eckhardtii*, because the angle of insertion of the lateral veins is much less than in *Taeniopteris* (Remy and Remy, 1977). The affinity of the taxa from Bletterbach is unclear. Some groups (bennettitaleans, Pentoxylales) are not plausible because of their very different stratigraphic and geographic distribution. Because cuticle is preserved in our specimens it is unlikely that they represent ferns. This leaves two options: pteridosperms and cycads. Galtier and Broutin (2008) who described several taeniopterids from the Rabejac Formation (Artinskian, Cisuralian) of Lodève, southern France, classified such leaves as putative cycads.

Taeniopteris sp. A
Plate III, 1, 4, V, 1–4, 6

Description: Linear, entire-margined leaf with a thick midvein. The incomplete, up to 120 mm long and 21 mm wide leaf fragments have a 3.5–5 mm thick midvein (PAL870, Plate III, 1). The leaves are entire margined, the lamina is inserted to the upper part of the rachis, which is almost invisible from above. Lateral veins arise at 80–90° from the rachis and never bifurcate; they are mostly straight but slightly curved in apical direction just before reaching the lateral margin; the density of the veins is 15–18 per centimetre at the lateral margin (PAL830, Plate III, 4).

The leaves are amphistomatic with a thicker cuticle and less stomata on the upper than on the lower side. Epidermal cells are slightly elongate and bear papillae (PAL870, Plate V, 1). The epidermal cells of the upper leaf surface are smaller and slightly more elongate (30–54 × 10–20 μm, mean 35 × 14 μm) than those on the lower surface (24–50 × 16–24 μm, mean 40 × 21 μm). Papillae are more common on the upper leaf surface (PAL870, Plate V, 2, 3). Stomata are irregularly scattered and less frequent on the upper leaf surface than on the lower surface, where they are arranged in irregular rows (PAL870, Plate V, 6). Guard cells are sunken and surrounded by 6–7 (rarely 8) subsidiary cells. Subsidiary cells are isodiametric and smaller than normal epidermal cells (12–28 μm, mean 19 μm) and covered by thick papillae, partially overarching the stomatal pit on the upper cuticle (PAL870, Plate V, 1–3).

Comparison: The specimens resemble *Lesleya* (al. *Taeniopteris*) *eckhardtii* except for the almost perpendicular angle at which the veins arise from the stout rachis (acute in *Lesleya*). *Lesleya eckhardtii* specimens from the English Zechstein (Wuchiapingian; Stoneley, 1958) resemble our material because of the parallel (undivided) and apically inclined lateral veins (60°), although the number of veins per centimetre is lower (8–9); we do not agree with Stoneley (1958) that the English specimens would fall within the variability of *L. eckhardtii* from the Germanic Basin because of the more acute angle of the lateral veins in the latter (40–60°). *Taeniopteris* sp. A resembles *Taeniopteris coriacea* Göppert 1864–65 from the Broumov Formation (upper Asselian, Cisuralian) of the Intrasudetic Basin, northern Bohemia (Czech Republic), in the perpendicularly arising lateral veins but the latter differs in its smaller size (lamina 18.5 mm wide, midvein about 2 mm wide) and the delicate lateral veins forking at the base and/or in the middle part of the lamina in the latter. In *Taeniopteris fallax* Göppert 1864–65 also originally described from the Broumov Formation, Intrasudetic Basin, the midvein decreases noticeably in width throughout the lamina, the dense (c. 40 per centimetre according to Wagner and Martinez Garcia, 1982) lateral veins always fork both at the base and in the middle of the lamina. *Taeniopteris abnormis* Gutbier 1835 (= *Taeniopteris multinervis* Weiss 1869; see Barthel, 1976; Barthel et al., 2010), originally described from the Rotliegend of Saxony has a rounded apex and a broad midvein (5–7.5 mm), covered with widely spaced glands; numerous delicate lateral veins arise perpendicularly from the thick midvein. *Taeniopteris doubingeri* Remy et Remy 1975 from the Millery Formation (Sakmarian, Cisuralian) of the Autun Basin, France, is a bipinnate form with narrow, lanceolate segments and a thick midvein with secondary veins arising at an angle of 70–75°, bifurcating several times. Bercovici et al. (2009, pl. III, 6) figured a specimen as *Taeniopteris* sp. 1 from the "upper Permian" (?upper Guadalupian, more likely Lopingian) of Minorca, Balearic Islands, Spain. Unfortunately, the fragment is very small (half of the lamina is 13 mm wide, the midvein is 2.5 mm wide, veins about 21/cm) and no bifurcations are visible on the parallel veins. The fragmentary preservation of this specimen does not allow further comparisons.

Distribution: This species has been collected from the new bed at Bletterbach and from "Butterloch-Taubenleck" (collected from loose blocks below the marine horizon).

Taeniopteris sp. B
Plate III, 2–3, 5; Plate V, 5, 7

Material: NMS PAL833, 844, 963, 1013, 1411, L2043, UU 16980, 23764, 23771, 23772, 23783, 23784, 23785, 23786, 23787, 23804, 23806.
Description: Entire-margined leaves with a stout midvein. The leaf fragments are up to 60 mm long; half of the lamina is usually up to 35 mm wide (PAL 844, Plate III, 2); in one specimen half of the lamina is 65 mm wide (PAL833). The midvein is up to 6 mm wide. The lamina is inserted laterally or to the upper side of the midvein. Specimens showing the entire width of the lamina have not been found but it can be assumed that the leaf may have been c. 70–90 mm wide. The lateral veins arise at an angle of 70°, slightly arch, then run almost perpendicularly to the lateral margin and that is reached at an angle of 80–90°, with a density of 12–18 veins per centimetre (PAL963, UU 23764, 16980, Plate III, 5). Some lateral veins fork once close to the midvein.

The leaf is amphistomatic with very thin cuticles. The epidermal cells of the upper surface are isodiametric (20–45 μm in diameter, mean 34 μm) and covered by papillae; the epidermal cells of the lower surface are more elongate (45–60 × 22–26 μm in diameter, mean 51 × 24 μm), with thickenings but without papillae (UU 23786, Plate V, 5). Stomata monocyclic, sunken and protected by 5–6 papillae of the subsidiary cells; the guard cells are sunken and covered by papillae of the 5–7 subsidiary cells. The subsidiary cells are similar to the epidermal cells of the upper surface, but slightly smaller (15–33 μm in diameter, mean 22 μm). The stomata are arranged in irregular rows (UU 23786, Plate V, 5, 7).

Comparison: In *Taeniopteris* sp. 1 sensu Galtier and Broutin (2008) from the red beds of Rabejac Formation (Artinskian, Cisuralian) in Lodève (France), the veins arise also at c. 70°, curve outwards and seem to reach the margin perpendicularly (the margin is covered in the specimen illustrated by Galtier and Broutin, 2008, fig. 4A); the visible part of the half lamina measures c. 30 mm and the midvein is very thick. This species from Lodève might be conspecific with *T.* sp. B. The specimens figured by DiMichele et al. (2001, figs. 5–7) from the lower Pease River Group (lower Guadalupian) of the United States are too fragmentarily for detailed comparison. *Taeniopteris coriacea* differs from *T.* sp. B in being smaller (lamina 18.5 mm wide, midvein about 2 mm wide) with delicate lateral veins forking at the base and/or in the middle part of the lamina. In gross morphology, *T.* sp. B resembles some fragments described as *Taeniopteris* cf. *fallax* by Wagner and Martinez Garcia (1982, pp. 279–80, fig. 5b–c, 6a–c) but differs in width (up to 140 mm) and the density of the lateral veins (40/cm). In *T. fallax* the lateral veins always fork both at the base and in the middle part of the lamina with densely inserted veins. *Taeniopteris abnormis* has a rounded apex and a thick rachis (5–7.5 mm), covered with glands; numerous delicate lateral veins arise perpendicularly from the thick midvein. *Taeniopteris doubingeri* differs in being bipinnate with narrow, lanceolate segments and a thick midvein with secondary veins arising at an angle of 70–75° and bifurcating several times.

Distribution: This species occurs in three exposures of the cuticle bed, called respectively “Butterloch R4” “Butterloch 3” and “Butterloch 4”, kept in the Utrecht collection and it also occurs in the new plant horizon.

Fragment of a cycad-like leaf?
Plate III, 6

Description: A fragment (PAL1003, Plate III, 6) of a pinnate leaf, 16 mm long and 23 mm wide, with a 2.5 mm wide rachis, with incompletely preserved, 6–17 mm long and 2–4 mm wide segments, arising at an angle of 40°.

Material: NMS PAL1003.

Remarks: The very fragmentary nature and the poor preservation of this specimen without cuticle do not allow precise assignment. Several species of cycad-like leaves, assigned to four genera, have been described from the Pennsylvanian and Permian of the Northern Hemisphere. Most species have been attributed to *Pterophyllum*, including six species from Europe (see Pott et al., 2010). *Pterophyllum* has recently been redefined to accommodate bennettitalean foliage only (Pott et al., 2007a,b). A bennettitalean affinity could not be demonstrated for any of the species reported from the Palaeozoic. One species from China previously assigned to *Pterophyllum* has cyclocytic stomata and was transferred to *Pseudoctenis* Seward 1911, a genus for cycadalean foliage. Cuticles have been reported from a few other species but these cuticles are very fragmentary and do not indicate a bennettitalean affinity (Pott et al., 2010). All Palaeozoic *Pterophyllum* species probably represent cycadalean rather than bennettitalean foliage. Our specimen does not resemble any of these forms; they are all much larger and typically have much broader leaf segments with parallel veins. The pinnate leaf from Wuchiapingian strata of Mölten/Meltina (Italy) assigned to *Pterophyllum* (Krainer, 2000, p. 74, fig. 124) is also much larger, c. 60 cm long and 30 cm wide with a forked axis and 15 cm long and 1 cm broad segments. *Plagiozamites* Zeiller 1894 is another problematic taxon that is cycad-like but it could also represent noeggerathialean foliage. *Plagiozamites bellii* Schweitzer, 1986 from the Marl Slate (Wuchiapingian) of England has spatulate, much larger (90 × 15 mm) segments that seem to be helically arranged and are inserted at an angle of 80°. According to Schweitzer (1986) this species might be a conifer rather than a cycadophyte. Stoneley (1958) described a single spe-ci-men from the Marl Slate with a very poorly preserved cuticle and provisionally assigned it to *Pseudoctenis*. This species, *Pseudoctenis middridgensis*, is superficially similar to our species because the segments arise at a similar angle (c. 40°), but the strongly decurrent segments are much larger (40 × 4.5 mm) and have two veins that bifurcate once or twice.

4. Comparisons with other Permian floras of the Alps

Only few floras from the Southern Alps are of Lopingian age, i.e., Mölten/Meltina (Fritz and Krainer, 1999; Krainer, 2000), Cuecenes (e.g., Florin, 1964; Leonardi, 1968), various localities in the Recoaro area (e.g., Clement-Westerhof, 1984; Aspmair and Krainer, 1998; Fritz and Krainer, 2006) and Bletterbach (e.g., Clement-Westerhof, 1984, 1986, 1987; Poort and Kerp, 1990; Kustatscher et al., 2012). These floras are all dominated by conifers and only few have yielded pteridosperm remains; *Germaropteris martinsii* has been found in Cortiana and Ulbe near Schio in the Vicentinian Alps, and in Bletterbach. Other, mostly older reports (e.g., Gümbel, 1877, 1879; Rothpletz, 1880) cannot be confirmed due to the lack of descriptions and adequate illustrations; it appeared to be impossible to retrieve the actual specimens, they seem to be lost. Most taxa are only mentioned in species lists, without descriptions and illustrations; in some cases exact locality data are unknown.

The Artinskian–Kungurian flora from the Collio Formation of upper Val Trompia is much older than the Bletterbach Flora (Remy and Remy, 1978; Visscher et al., 2001). Nevertheless, this conifer-dominated flora is of considerable interest, because it yielded one pteridosperm that is also present at Bletterbach, *Sphenopteris suessii*. The Kungurian flora of Tregiovo in the upper Val di Non is also dominated by conifers, including remarkably large *Ullmannia*- and *Pseudovoltzia*-like forms, and comprises a fragmentary taeniopterid that was identified as *Lesleya eckhartii* (Remy and Remy, 1978; Visscher et al., 2001), a species well known from the German and English Zechstein. Other more recent records of ferns, pteridosperms and presumed cycads (e.g., Leonardi, 1948; Krainer, 2000) cannot be confirmed due to the poor preservation of the material. The occurrence of sphenopsids (i.e. *Annularia*, *Calamites*, *Stylocalamites*) reported by Krainer (2000) from Mölten also cannot be justified since characters typical for these genera are missing in the material he illustrated.

Plate V. Scale bar 50 μm.

1. *Taeniopteris* sp. A, lower cuticle with elongated to slightly isodiametric epidermal cells, stomata with six papillate subsidiary cells (NMS PAL 870)
2. *Taeniopteris* sp. A, stomata of upper cuticle with six papillate subsidiary cells, papillae covering the stomatal pit (NMS PAL 870)
3. *Taeniopteris* sp. A, stomata of lower cuticle with six papillate subsidiary cells (NMS PAL 870)
4. *Taeniopteris* sp. A, lower cuticle with slightly elongated epidermal cells, stomata scattered (NMS PAL 870)
5. *Taeniopteris* sp. B, lower cuticle with elongate epidermal cells, stomata monocyclic and surrounded by 5–6 subsidiary cells (UU 23786)
6. *Taeniopteris* sp. A, details of lower cuticle with two stomata surrounded by papillate subsidiary cells (NMS PAL 870)
7. *Taeniopteris* sp. B, upper cuticle with papillate, isodiametric epidermal cells (UU 23786).

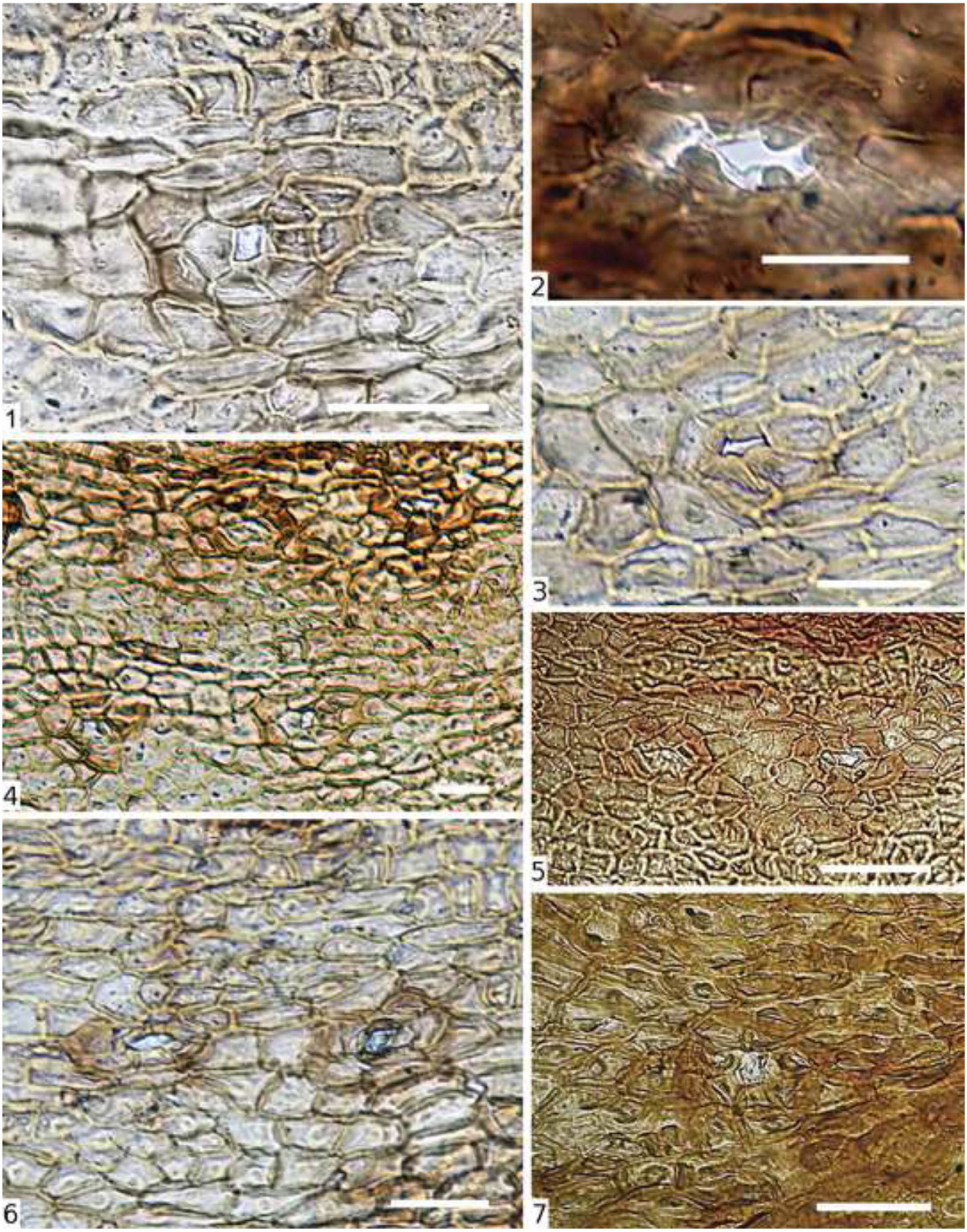
1
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Table 1
Occurrences of sphenopsids, pteridosperms and putative cycadaleans in the German and English Zechstein, and the Southern Alps, Italy.

	Germany						UK	Italy
	Gera	Mansfeld	Ilmenau	Richelsdorf	NE Hesse	Lower Rhine	northern England	Bletterbach
Neocalamites mansfeldicus		+		+		+	+	
?Equisetites sp.					+			+
Germaropteris martinsii	+	+		+	+	+	+	+
Sphenopteris sp.								+
Sphenopteris dichotoma	?	+		+			+	
Sphenopteris geinitzii	+		+	+				
Sphenopteris kukukiana						+		
Sphenopteris patens	+	+		+				
Sphenopteris suessii								+
Lesleya eckhardtii	+	+		+			+	
Taeniopteris sp. A								+
Taeniopteris sp. B								+
pinnae with alethopteroid pinnules								+
Plagiozamites bellii							+	
Pseudoctenis middridgensis							+	

5. Comparisons with other Lopingian floras of Europe

Floras from the basal part of the German Zechstein have been described as early as the 18th and early 19th centuries (Mylius, 1709; Waldin, 1778; Ullmann, 1803; Germar in Kurtze, 1839). Plant fossils occur in the marine Kupferschiefer in the classical mining areas, e.g., around Mansfeld, Ilmenau and Richelsdorf, in marls and limestones, e.g., near Gera, Geismar (NE Hesse), the Lower Rhine, and in silty to marly basin margin sediments, e.g., Frankenberg (NE Hesse). Plant fossils from the typical Kupferschiefer lack cuticle. However, they are commonly well preserved in marly facies, e.g., in Gera and the Lower Rhine, where carbonate concretions with three-dimensional, anatomically preserved plants occur (e.g., Solms-Laubach, 1884; Schweitzer, 1962, 1963). Pyritized, mummified and charred plant remains from Geismar (NE Hesse) also give valuable information on the anatomy of Zechstein plants (Uhl, 2013). Comprehensive reviews on the flora of the German Zechstein were given by Schweitzer (1968, 1986), Haubold and Schaumberg (1985), Brandt (1997) and Uhl and Kerp (2002). The floras from the German Zechstein are the most diverse Lopingian floras currently known from Europe, although the number of species is low. Comparable, reasonably diverse floras have been described from the westernmost part of the Zechstein Basin in NE England (Stoneley, 1958; Schweitzer, 1986).

Sphenophytes, pteridosperms and putative cycadaleans all occur in the German and English Zechstein and the Bletterbach flora of Italy (Table 1). All these floras are strongly dominated by conifers, especially *Ullmannia*, *Pseudovoltzia* and *Quadrocladus*. Other conifer taxa are restricted to the Southern Alps, i.e., *Ortiseia*, *Majonica* and *Dolomitia*. However, it may be assumed that at least some of these also occurred in the German and English Zechstein, e.g., *Ortiseia*, because its prepollen, *Nuskoisporites dulhuntyi* Potonié et Klaus 1954, has a much wider geographical distribution. Forms described as *Culmitzschia* Ullrich 1964 from the German Zechstein may be identical to *Ortiseia*. Preliminary analyses of bulk-macerated samples from the Zechstein of Gera have shown that *Ortiseia* and possibly also *Majonica* indeed occur in the German Zechstein (Bödige, 2007). Sphenophytes are relatively rare in the German and English Zechstein and in the Southern Alps. Macrofossils of lycopsids have never been encountered; however, their presence is evidenced by the palynological record including megaspores. *Germaropteris martinsii* is the only pteridosperm that is known from nearly all regions (Table 1). Sphenopterids have been reported from all regions, although being represented by different species. Taeniopterids also occur in all regions, but *Lesleya eckhardtii* is restricted to Germany and England. *Plagiozamites bellii* and *Pseudoctenis middridgensis*, both from Marl Slate of England, are two problematic taxa whose natural affinity remains unclear. The presence of pinnae with alethopteroid pinnules in the Bletterbach flora is remarkable, because similar forms have not been described from other European Lopingian occurrences. Ginkgophytes are relatively rare elements in Lopingian floras. *Baiera digitata* (Brongniart 1828) Heer 1876 is the most common ginkgophyte in the Kupferschiefer. It has been described from England (Stoneley, 1958), Germany (e.g., Weigelt, 1928; Schweitzer, 1962) and it probably also occurs in Bletterbach (Kustatscher et al., 2012). An additional *Baiera* species, *Baiera mansfeldensis* Bauer et al., 2013, has been found in the Kupferschiefer flora of Saxony-Anhalt (Germany), together with few specimens of the putative ginkgophyte taxon *Esterella gracilis* Boersma et Visscher, 1969 (Bauer et al., 2013). A very small Zechstein flora containing only *Ullmannia* has been reported from Belgium (Florin, 1954). The small conifer-dominated floras from the Holy Cross Mountains and Wola Murowana (Gałicia), Poland (Czarnocki and Samsonowicz, 1913; Pajchlowa and Wagner, 2001) and Hungary (Heer, 1876) are clearly in need of revision and cannot be discussed further here. Bercovici et al. (2009) described a small flora from the Cala del Pilar (?upper Guadalupian, more likely Lopingian) of Minorca, Balearic Islands, Spain, which apart from a single putative cycad leaf fragment (Bercovici et al., 2009, pl. III, 6) consists exclusively of conifers.

Although the number of species is small, the Bletterbach flora ranks, with a range of conifers (Clement-Westerhof, 1984, 1986, 1987), ginkgophytes (Kustatscher et al., 2012) and sphenopsids, pteridosperms and putative cycadophytes described here, among the most diverse floras currently known from the Lopingian of Europe. Apart from the diversity, the preservation, in many cases with well-preserved cuticles, is of particular interest, because cuticles enable whole plant reconstructions even where specimens are fragmentary and dispersed (Clement-Westerhof, 1984, 1986, 1987; Poort and Kerp, 1990). The newly discovered macroscopic remains reported by Kustatscher et al. (2012) and in this paper add an extra dimension, because they give more information on the habitus of the plants.

6. Comparisons with Permian peri-Palaeotethyan floras

The new flora derives from a site not too far from the margin of the Palaeotethys. Therefore, it is of interest to compare this flora to Permian floras from perigondwanan terranes and the southern margin of the western Palaeotethys. Permian floras have been described from Morocco, Turkey, Jordan, Iraq, Saudi Arabia and Oman.

The Moroccan floras are dated as Kungurian (late Cisuralian) and comprise, apart from calamites and pecopterids, a variety of conifer and callipterid species, most of them being well known from the Cisuralian of Europe. These are the most dominant forms. However, remarkable is the common occurrence of ginkgophytes, a group that is normally rare in older Permian strata but well represented in the Zechstein and Bletterbach flora (Bauer et al., 2013, in prep.). Other remarkable constituents include a Cathaysian form (*Protoblechnum*), an Angaran (*Mostotchkia*) and Gondwanan elements (putative Glosssopterids) (Broutin et al., 1998). The flora from Hazro, eastern Anatolia (Turkey), which predominantly consists of sphenopsids and ferns, is a mixture of mainly Cathaysian taxa with some Gondwanan elements; in addition a few Angaran and Euramerican taxa occur (Wagner, 1959, 1962; Archangelsky and Wagner, 1983). The absence of conifers and the high diversity of pecopterids is remarkable. The top of the formation conformably underlying the plant-bearing beds has been dated as earliest Capitanian, Guadalupian (Stolle, 2010). A small flora, exclusively consisting of Cathaysian taxa, is known from the upper Permian of western Iraq (Čtyroký, 1973). In central Saudi Arabia (Qasim Province), two members of the Khuff Formation (Guadalupian–Lopingian) have yielded good megafloras. The Unayzah Member has a rich flora with several Cathaysian elements, dominated by ferns and sphenopsids (El-Khayal et al., 1980; Lemoigne, 1981a,b; Hill and El-Khayal, 1983; El-Khayal and Wagner, 1985; Hill et al., 1985; Wagner et al., 1985). The overlying Khuff Member yielded taeniopterid leaves and Euramerican-type conifers (El-Khayal and Wagner, 1985). The Gharif Formation (Wordian, Guadalupian) in central Oman (Broutin et al., 1995; Berthelin et al., 2003, 2006) has yielded a flora consisting of typical Cathaysian and Gondwanan taxa, with a few Euramerican elements. The latter include walchian conifers similar to those known from Cisuralian strata of Europe and Morocco. Several outcrops in the Um Irna Formation exposed in the Dead Sea region, Jordan, have yielded macrofloras. Most spectacular is the type section of the formation with abundant, excellently preserved leaf remains of four species of *Dicroidium*, a typical Gondwanan element. In addition, a taeniopterid leaf was found (Kerp et al., 2006; Abu Hamad et al., 2008). During recent fieldwork *Dicroidium* was also found in at least three other nearby localities. One of these localities also yielded a few fragmentary Gondwanan conifers. Mustafa (2003) described a small flora from the same formation with several typical Cathaysian elements. The presence of representatives from several floral provinces is also confirmed by the palynological record (Stephenson and Powell, 2013). The age of the Um Irna Formation was originally indicated as late Permian, but these palynological studies (Stephenson and Powell, 2013) indicate a Wordian–Capitanian to early Wuchiapingian (Guadalupian to early Lopingian age).

Most Permian floras from perigondwanan terranes and the southern margin of the western Palaeotethys thus appear to be older than the Bletterbach flora, which is dominated by conifers (Clement-Westerhof, 1984, 1986, 1987; Visscher et al., 2001; Kustatscher et al., 2012). Remarkable is the absence or rareness of conifers in several floras from the southern margin of the Palaeotethys and the northernmost part of Gondwana. When present, they are typical walchian conifers, like those known from the Cisuralian of Europe (Morocco, Oman) or Gondwanan forms (Jordan). All floras from the southern margin of the Palaeotethys show a mixture of elements from several floral provinces, mainly Cathaysia and Gondwana, especially those from the Middle East. No typical Gondwanan or Cathaysian taxa have been identified from the Bletterbach section. The most common pteridosperm from Bletterbach, *Germaropteris martinsii*, which is also known from the Zechstein Basin, has not been found in any of the associations from the Middle East. Although Bletterbach was not too far from the northern margin of the Palaeotethys, the macroflora shows no influence from Gondwana and Cathaysia. The Bletterbach flora is a typical European flora, which is, as has been shown above, well comparable to floras from the Zechstein Basin.

7. Concluding remarks

The conifer-dominated Wuchiapingian floras of Europe are often considered to have grown under semi-arid to arid conditions, based on the presence of xeromorphic features, such as thick cuticles, the presence of papillae, sunken stomata that are commonly protected by overarching papillae and clear differences in cell size and stomatal density between the upper and lower leaf surfaces. Another indication is the foliar physiognomy. *Germaropteris martinsii* had relatively small fronds, compared to those of Cisuralian callipterids and Triassic *Lepidopteris* species, which probably are the closest relatives, but they were thick and fleshy. Conifers from this time interval also had thick and fleshy leaves in contrast to the typical narrow needle-like leaves known from the Cisuralian; walchian conifers from the Cisuralian had decurrent, narrow, needle-like leaves, whereas Lopingian walchians, i.e., *Ortiseia*, had broad, thick, non-decurrent leaves. The strong dominance of gymnosperms is also a clear indication for dry conditions. However, it should be noted that all floras are to a greater or lesser degree allochthonous; most of the typical Zechstein floras even occur in marine sediments or in marginal marine deposits and some degree of sorting cannot be excluded. Nonetheless, the palynological record also shows a strong dominance of drier elements, but certain taxa such as lycopsids that are represented in the palynological record are definitely missing in the macrofloral record.

Although Lopingian floras are dominated by conifers – some smaller floras contain conifers exclusively – and although *Germaropteris martinsii* is represented in virtually all associations, there seem to be considerable differences regionally. As noted before, some conifers (*Ullmannia*, *Pseudovoltzia*, *Quadrocladus*) are known from the Zechstein Basin (Germany and England), where the first two genera are dominant, and from the Southern Alps, where they are just minor constituents. The latter floras are characterized by a dominance of *Ortiseia*, a genus initially considered absent from the floras of the Zechstein Basin but later identified in the Zechstein Basin based on both the palynological record (see e.g., Kerp, 1996), and macrofossils in at least one association (Gera-Trebnitz: Bödige, 2007). The situation seems to be similar with regard to the non-coniferous taxa. Most groups, although represented by different species, are represented in both the Zechstein floras and in the Southern Alps (sphenopterids, taeniopterids, ginkgophytes) with the exception of the alethopteroid foliage that has so far only been found in the Southern Alps. Palynological associations show that differences are quantitative rather than qualitative (Kerp, 1996, 2000).

Cuticles show that there are other differences, even within the species that are known from the Zechstein Basin and the Southern Alps. Comparing the cuticles of taxa that are known from both regions, it is remarkable that the cuticles of the same species are much thicker in the Southern Alps than in the Zechstein Basin. *Germaropteris martinsii* from the Southern Alps has thick cuticles, mostly with very prominent papillae, whereas specimens from Germany have thinner cuticles and papillae are less prominent or even absent on normal epidermal cells and occur only on subsidiary cells. Cuticles are even thinner and true papillae are absent in the English material; only slight thickenings on the subsidiary cells are present. *Pseudovoltzia liebeana* shows the same variation in thickness and ornamentation of the cuticle (Kerp, 1996). These differences show that xeromorphic features are much more pronounced in the material from the Southern Alps than in the material from the Zechstein Basin, although variation is also evident within the latter region. These variations are due either to ecological or climatic differences, or to a combination of both. Xeromorphic features are not necessarily an indication of dry conditions. Also plants growing in brackish habitats and plants exposed to brackish and salt water, either edaphically, by occasional flooding or salt water spray as well as plants growing in peat bogs on low-nutrient soils or with reduced pH values often show such typical adaptations (e.g., Wartmann, 1969; Kerp, 1990; Pott and McLoughlin, 2009, 2011; Stull et al., 2012). Because many Zechstein floras are found allochthonous in marine and marginal marine settings cautious palaeoenvironmental interpretation is required. However, plants occur in a terrestrial setting in the Bletterbach section. The Gröden/Val Gardena Sandstone is almost entirely terrestrial, with rooted soils and caliche horizons, with exception of the cephalopod bed at the waterfall, which represents a short-term marine transgression. The plant remains are commonly fragmented due to fluvial transport and occur in sandy channel deposits. Charred plant remains indicating wildfires are also known (Uhl et al., 2012). Therefore, it is most likely that xeromorphic features are indeed indicative of climate. The differences between the floras from the Zechstein Basin and the Southern Alps reflected in the cuticles, and possibly also in the quantitative composition of the flora, are likely an expression of a climatic gradient. Sedimentological data also indicate semi-arid to arid conditions during the deposition of the Gröden Formation (Massari et al., 1988; Ori, 1988). The sphenopsids probably grew in small, more humid biotopes (Schweitzer, 1986). Conifer wood shows distinct growth rings suggesting regular periodic changes, probably an alternation of more-humid and drier periods (Schweitzer, 1968, 1986).

In Europe and North America, the Permian shows a general, progressive trend towards drier climates, which is expressed in both the palaeofloras and palaeosols (e.g., Kerp, 2000; Roscher and Schneider, 2006; Montañez et al., 2007). Although the general trend is clear, it was not a consistent shift, but drier periods alternated with more humid to wet phases, particularly during the Cisurlaian. The aridification in equatorial Pangea started in the late Westphalian, near the Bolsovian–Asturian boundary (Van Hoof et al., 2013; DiMichele, 2014) with an overall pattern of wet periods being less wet and dry periods being more dry during glacial–interglacial cycles. Aridification became more widespread in the Asselian but more humid to wet phases persisted until at least Artinskian time (Roscher and Schneider, 2006; Montañez et al., 2007). In the Lopingian, a cyclicity can be recognized with a wet phase in the middle Wuchiapingian (Legler et al., 2011; Legler and Schneider, 2013). This wet phase marks the main Zechstein transgression, which is preceded by pre-Zechstein ingressions in late Capitanian and the early Wuchiapingian (Legler and Schneider, 2013). Although it is speculative, the marine cephalopod bed within the Gröden/Val Gardena Sandstone might reflect this major sea level change. In the Germanic Basin plant fossils occur in the Kupferschiefer and in the marls and sandstones immediately underlying the Kupferschiefer as well as in shallow water and terrestrial equivalents. The red beds underlying the basal Zechstein do not contain any plant fossils. In the Bletterbach section, they mainly occur just below and just above the cephalopod bed. They are much rarer to even absent in the upper part of the formation, where evaporites (gypsum) and pedogenic carbonates are common. However, immediately below the top of the Gröden/Val Gardena Sandstone, which is overlain by the marine Bellerophon Formation, macroscopic plant remains re-appear in the form of plant debris, similar to but less frequent than in the cuticle bed above the cephalopod bed. This would suggest that the occurrences of plants are related to sea-level changes and the corresponding environmental changes, even though the climate was semi-arid to arid throughout. Plants appear to be most common immediately before and after the maximum transgression or sea-level high-stand.

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