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Research paper

A new flora from the Upper Permian of Bletterbach (Dolomites, N-Italy)

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ABSTRACT

A new fossiliferous horizon from the famous Bletterbach area is described. The new megafossil locality of late Permian age yields well-preserved plant megafossils, as well as cuticles and *in situ* pollen. In the flora representatives of the horsetails, seed ferns (*Sphenopteris*, *Lepidopteris*, *Peltaspermum*), putative cycadophytes (two types of *Taeniopteris*), ginkgophytes (three different leaf types) and conifers (*Ortiseia*, *Pseudovoltzia*, *Quadrocladus*, *Pagiophyllum*) were distinguished. Remains of doubtful botanical attribution comprise *Dicranophyllum*-like leaves and *Leptostrobus*-type of female fructifications as well as permineralized wood and charcoal. Remains of lycophytes reported from the Bletterbach cannot be confirmed. Some of these groups are recorded for the first time from the Bletterbach.

1. Introduction

Late Permian floras are scarce throughout Europe and North America, and thus still incompletely understood. Our knowledge on late Permian floras from Europe is mainly based on records from the European Zechstein Basin. This basin extended from the British Isles, through the North Sea, the Netherlands, Denmark, Germany and Poland into the Baltic region. Particularly the German Zechstein has yielded a number of classical macrofloras; for overviews the reader is referred to Schweitzer (1968, 1986), Haubold and Schaumberg (1985), and Uhl and Kerp (2002).

Most of the late Permian Euramerican floras are compression floras. The classical Kupferschiefer floras from Thuringia and Hessen (e.g., Weigelt, 1928, 1930) do not yield cuticles, but several others developed in a marginally marine facies do, notably the floras Lower Rhine Embayment (Gothan and Nagalhard, 1922; Schweitzer, 1960), North-Eastern Hessen (Uhl and Kerp, 2002) and northern England (Stoneley, 1958). Few localities of these areas also yielded anatomically preserved material (Solms-Laubach, 1884; Schweitzer, 1962, 1963). Dispersed, bulk-macerated cuticles have been described from Saxony (Ullrich, 1964).

Even though the number of plant-bearing Zechstein localities is limited, information on late Permian floras from southern Europe is even scarcer. Late Permian floras are known from a few localities in the Western Dolomites (South Tyrol) and Vicentinian Alps, northern Italy (e.g., De Zigno, 1862; Massalongo, 1863; Geinitz, 1869; Visscher et al., 2001), the Balearic Isles (Bercovici et al., 2009) and the Esterel Massif of Southern France. An overview of this latter rather poorly preserved, low-diversity flora is not available, but a few taxa have been described and illustrated in Boersma and Visscher (1969), and in Remy and Remy (1978). Nevertheless, studies of bulk-macerated dispersed cuticles, mainly from the Bletterbach locality in the western Dolomites, have provided very detailed information on a selected number of taxa, mostly conifers (Clement-Westerhof, 1984, 1987, 1988; Poort and Kerp, 1990).

The first reference to Permian plant remains from South Tyrol is from Gümbel (1877), who reported *Voltzia hungarica*, *Baiera digitata*, *Ullmannia bronnii*, *U. geinitzii*, *Carpolithes*, *Calamites* or *Equisetites* and a fern fragment from the "Grödner Sandstein" near Neumarkt/Egna. Other localities with plant fossils from the Gröden Sandstone (= former Grödner Sandstein; Italian: Arenaria di Val Gardena) in South Tyrol are Auer/Ora (Leonardi, 1948), Cuecenes (Charrier, 1964; Florin, 1964) and the Seiser Alm/Alpe Siusi (Jung, 1977).

Perwanger (1946) was the first to mention plant fossils from the Bletterbach gorge, including a "*Lepidodendron*-Stengel". During the

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following years, Leonardi studied the Butterloch area of the Bletterbach Gorge, which he originally considered early-middle Permian in age. In 1948 he described and figured fossil tree trunks assigned to *Lepidodendron* from the northern side of the Weisshorn/Corno Bianco. From the Bletterbach-Butterloch he mentioned "*Lepidodendron* cf. *sternbergi* Lindley et Hutton vel *Schizolepis permensis* Heer; *Lepidodendron* cf. *veltheinianum* Sternberg, *Lepidodendron* sp., *Lebachia* (=*Walchia* auct.) *laxifolia* Florin and *Lebachia* (?) sp." (Leonardi, 1948, pl. 1, 1–9). In the following years, he continued the studies in this area and collected several more plant fossils, especially conifer shoots and cones (Leonardi, 1951, 1968).

Although most remains so far known were very fragmentary preserved, cuticle preservation is excellent, as was shown by Clement-Westerhof (1984, 1986, 1987) and Poort and Kerp (1990). Clement-Westerhof (1984, 1986, 1987) described and figured several conifers from cuticle horizons at Butterloch and Taubenleck (both in Bletterbach gorge), based on small remains with exceptionally well-preserved cuticles: *Ortiseia leonardii* Florin, 1964, *O. jonkeri* Clement-Westerhof, 1984, *O. visscheri* Clement-Westerhof, 1984, *Dolomitia cittertiae* Clement-Westerhof, 1987, ovuliferous dwarf-shoots of *Pseudovoltzia liebeana* (Geinitz) Florin, 1927, *P. sjerpii* Clement-Westerhof, 1987. She also described *in situ* pollen such as *Nuskoisporites* Potonié et Klaus, 1954 from *Ortiseia* Florin, 1964 and *Lueckisporites* Potonié et Klaus, 1954 from *Majonica alpina* Clement-Westerhof, 1987 (Clement-Westerhof, 1974, 1988). Poort and Kerp (1990) described foliage and ovuliferous discs from the Bletterbach of the seed fern *Peltaspermum martinsii* (Germar) Poort et Kerp, 1990. During the last few years, studies on cuticles from Bletterbach focused mostly on paleoecological and paleoclimatic reconstructions (e.g., Uhl and Kerp, 2005; Vörding and Kerp, 2008).

Bulk macerations reveal a flora strongly dominated by conifers; additional elements include pteridosperms and ginkgophytes (Kerp and Kustatscher, 2005). However, it should be noted that only gymnosperm cuticles are preserved because pteridophyte cuticles are very thin and thus have a low preservation potential. Therefore, the composition of the flora in bulk macerations is strongly biased towards gymnosperms with thick and resistant cuticles. However, palynological studies show that hygrophyllous taxa (especially ferns) are poorly represented (only up to 5%; Pittau, 2005). The spores in the assemblages are rare but moderately diversified and are represented by 27 different species (out of 97 species in total; see also Massari et al., 1994).

Of great importance is the discovery of well-preserved plant megafossils in a fossil-bearing lens from the lower part of the Gröden Sandstone of the Bletterbach locality a few years ago. This area is part of the UNESCO world heritage site Dolomites since 2009. Within the framework of a project initiated by the Museum of Nature South Tyrol and the Geoparc Bletterbach, several hundreds of plant fossils have been collected from 2003 to 2011. These are now stored at the Museum of Nature South Tyrol in Bozen/Bolzano. This is the first diversified late Permian flora with cuticles known from Northern Italy. As a result, it is now possible to elucidate the gross morphology of plant taxa that were hitherto only known from small remains and/or dispersed cuticles. The study of this new flora from Bletterbach will allow new insights in the late Permian flora of the Southern Alps, which appears to be much more diversified than previously thought. First studies about the new flora dealt with ginkgophyte leaves with putative seed-attachment (Fischer et al., 2010). This paper will provide a first, short overview of the newly found flora including some of the cuticles and a brief discussion of the geology of the locality.

2. Stratigraphic setting and age

The Bletterbach Gorge is located at the western edge of the Dolomites, between the villages Aldein/Aldino and Radein/Redagno (Fig. 1). The basal rocks in the gorge are andesites, rhyolitic lavas and ignimbrites of the Athesian Volcanic Group (Morelli et al., 2007). They belong to a caldera formed during the Cisuralian (early Permian), which had its centre northwest of the Bletterbach. The up to 2000 m thick volcanic succession has not been formed with a uniform accumulation rate during the whole period but in various intervals evidenced also by different volcaniclastic events throughout the succession (Morelli et al., 2007).

The Permian volcanites are overlain by an approximately 210 m thick sedimentary succession of the Grödner Sandstein/Arenaria di Val Gardena (in English it would be Gröden/Val Gardena Sandstone but since it was originally introduced by Richthofen, 1860 as Grödner Sandstein, we call it in the following text Gröden Sandstone). The boundary between the Athesian Volcanic Group and the Gröden Sandstone is probably indicated by an unconformity after a long period of subaerial erosion (Morelli et al., 2007), with a sedimentary hiatus of approximately 14 to 27 million years (Cassinis et al., 1999). The overlying Gröden Sandstone is characterized by red-greyish fluvial siliciclastics. The base of the Gröden Sandstone overlying the volcanic rocks is characterized by poorly sorted conglomerates, pebbly and muddy sandstones, and siltstones (Massari et al., 1988). Upwards alternations of fluvial siliciclastics, evaporites and mixed carbonate-siliciclastic deposits occur, reflecting environments of alluvial fans, braided rivers, shallow channels, coastal sabkhas and evaporitic lagoons or a shallow shelf (Italian IGCP 203, 1986; Ori, 1988). Gypsum occasionally occurs in the red mudstone, either as sparse nodules or as continuous layers interpreted as continental sabkha episodes (Massari et al., 1988). Paleosols may occur as well, represented by calcic soils, locally with vertic features (Wopfner and Farrokh, 1988), suggesting a warm to hot, semi-arid to dry-subhumid climate with strong seasonality (Cassinis et al., 1999). At about 80 m from the base of the succession, a general transgression can be observed by a change in colour (red to grey to blackish). The increasing marine influence is proven by sedimentary structures, such as wavy bedding or inclined heterolithic stratification, typical of a tidally-influenced coastal plain. The maximum transgression is characterized by a prominent, about 2 m thick marine, carbonatic bed (Cassinis et al., 1999), containing a sparse cephalopod fauna, including *Stearoceras* sp. (Broglio Loriga et al., 1988). The differences in lithology between the marine horizon, consisting of more erosion-resistant limestone, and the less resistant siltstones and sandstones below and above resulted in the formation of the waterfall in the Butterloch gorge. Grey to blackish mudstones crop out above the waterfall, with tidal-influenced deposits, and finally again cross-bedded shallow channel deposits, immature paleosols (entisols) representing the return of the continental conditions with emerged land.

The Gröden Sandstone is famous for its abundance and high diversity of ichnofaunas consisting of tetrapod footprints (e.g., Conti et al., 1975, 1977, 1979; Ceoloni et al., 1988; Wopfner, 1999). Several horizons yielded up to sixteen ichnotaxa belonging to various groups such as Gorgonopsia, Cynodontia, Lepidosauromorpha, Pareiasauridae and Rhynchosauroidea (Avanzini and Tomasoni, 2004). Typical Permian genera (e.g., *Ichniotherium*, *Hyloidichnus*), have been found in association with taxa displaying a clear Triassic affinity (e.g., *Rhynchosauroides*, *Dicynodontipus*) (Avanzini and Tomasoni, 2004; Avanzini et al., 2011).

The plant remains were collected from several levels in the Gröden Sandstone (Fig. 2). One mudstone horizon below and two immediately above the waterfall contain small twigs and leaves with perfectly preserved cuticles; these represent the "cuticle horizons" (e.g., Clement-Westerhof, 1984, 1986, 1987). Further below, the new fossiliferous horizon rich in large macroremains is less than one metre thick and characterized by medium- to coarse-grained greyish sandstones, sometimes with small, intercalated gypsum nodules. This locality is here termed "new megafossil locality", whereas the cuticle-bearing horizons are referred to as "Bletterbach Gorge". The designation "Bletterbach area" refers to finds from the Bletterbach of which the exact locality data are not known.

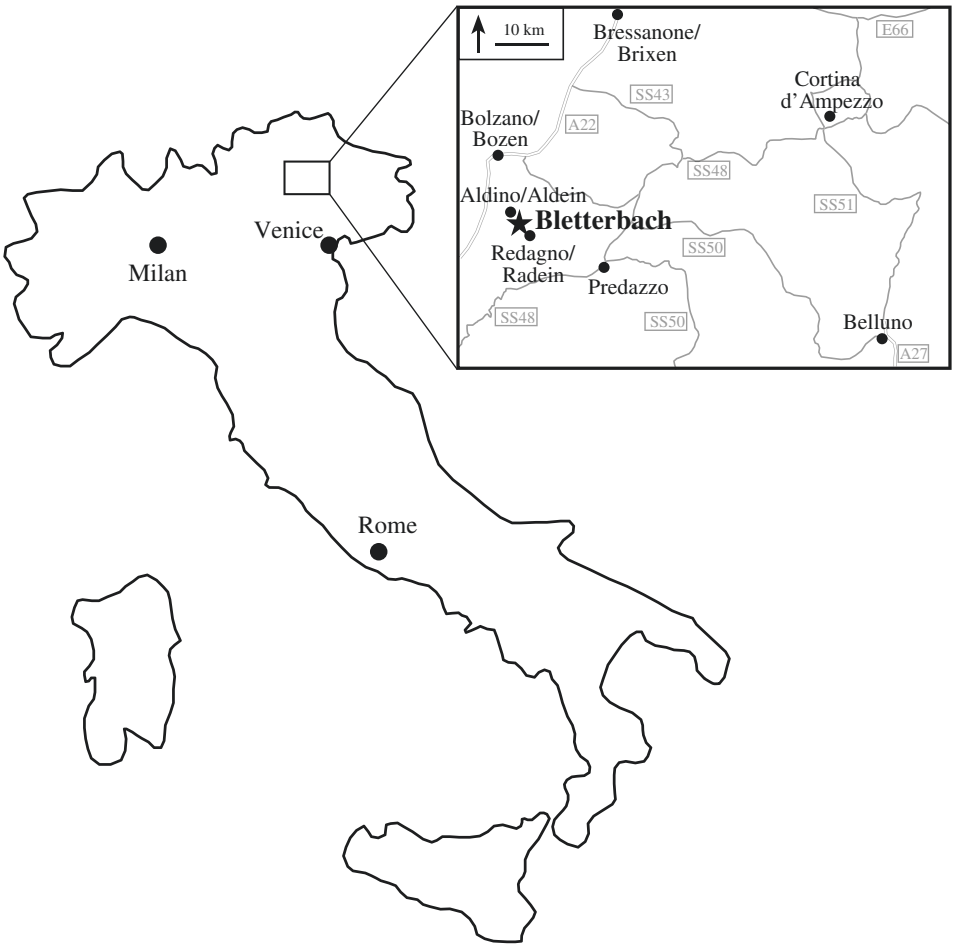


Fig. 1. Geographic position of the Bletterbach.

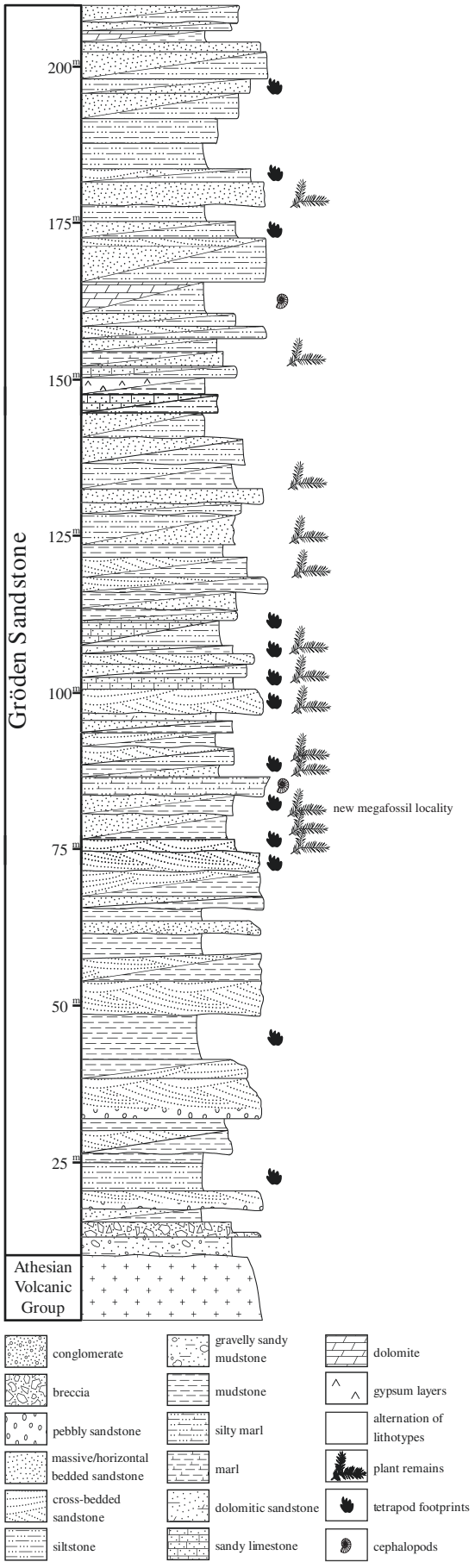
The transition of the Gröden Sandstone to the overlying Bellerophon Formation is an interfingering of fluvial and coastal/lagoonal deposits. The Bellerophon Formation is characterized by lagoonal dolomicrites rich in evaporitic gypsum ("*facies fiemmazza*" auct., Massari et al., 1988, 1994; Neri and Massari in Massari et al., 1999), followed by open-lagoonal dolomitic packstones ("*facies badiota*" auct.). The top of the Bellerophon Formation has a clearly transgressive character and is overlain by oolitic grainstones, which make up the lower part of the Tesero Horizon, the lowermost member of the Werfen Formation, in which the P/T boundary is positioned. The Werfen Formation (Induan–Olenekian) forms a transition towards a mixed carbonate-siliciclastic composition. The stratigraphic succession of Bletterbach ends with the upper Anisian Richthofen Conglomerate and a carbonate unit historically assigned to the Upper Serla Dolomite, but probably belonging to the Contrin Formation (Piero Gianolla, Marco Avanzini, pers. comm., 2009–10).

Radiometric data (U/Pb) carried out during the CARG geological mapping project suggested that the volcanic activity lasted for 11 million years, from about 284.9 ± 1.6 million years at the base to 274.1 ± 1.4 million years at the top; thus from the end of the Sakmarian, through the Artinskian to the beginning of the Kungurian (Avanzini et al., 2007; Marocchi et al., 2008). The exact age of the overlying Permian sedimentary succession is poorly constrained. Palynology suggests a late Capitanian to Changhsingian age for the Gröden Sandstone and the Bellerophon Formation (Pittau, 2005). However, according to Visscher (pers. comm., 2012) typical Guadalupian (Middle Permian) elements such as *Crucisaccites* are absent and the section could thus be restricted to the Lopingian. Also Cassinis and Ronchi (2001) questioned, for stratigraphic reasons, a Guadalupian age for part of the Gröden Sandstone. The tetrapod footprint fauna of the Gröden Sandstone of the Bletterbach has been attributed to the Wuchiapingian (late Permian; Avanzini et al., 2011). Since all horizons yielding fossil plants are above the first footprint level, the plant horizons would also be restricted to the Wuchiapingian. Lucas and Hunt (2006) proposed that the temporal gap between the early Permian ichno associations of the Tregiovo Beds and the Orobic Basin on one hand and the Bletterbach sequence on the other, the latter being rich in therapsids and pareiasaurs, must be "equal to at least the entire Guadalupian". If a Wuchiapingian age of the overlying Bellerophon Formation (Ceoloni et al., 1988) is confirmed, this would mean that the Gröden Formation represents only part of the Wuchiapingian, i.e. that it would have been deposited in less than 6 Ma. Further micropaleontological analyses (palynomorphs, foraminifera) might provide more details about the age of this formation and the new flora.

3. Material and methods

The plant fossils from the new macrofossil locality are up to 30 cm long and in most cases the preservation is good, yielding cuticles and *in situ* pollen. This makes a more precise taxonomic assignment possible, and a correlation with the small leaf and shoot fragments from bulk macerations and from the collections from the 1960s and 1970s stored at the Utrecht University, The Netherlands.

The material was studied under a dissecting stereomicroscope. Of some specimens cuticle preparations were made by maceration in Schulze's reagent ($KClO_3$ and 30% HNO_3) and neutralization in ammonium hydroxide (NH_4OH, 5%). Cuticles were mounted in glycerine jelly on microscope slides for light microscopic analysis and sealed



with paraplast (see Batten, 1999). Hand specimens were photographed with a Nikon Coolpix 990 digital camera. Cuticles were analysed with a Leitz Diaplan microscope and photographed with a Nikon DS-5Mc/Nikon DS-L2 digital camera.

The megafossil plant collection from the new horizon is stored at the Museum of Nature South Tyrol/Naturmuseum Südtirol in Bozen/Bolzano (Italy), as are the cuticle slides. They all have the specimen code "PAL". Specimens with the code "BUT" are stored in the collections of the Laboratory of Palaeobotany and Palynology, Utrecht, The Netherlands.

4. The flora

A preliminary systematic analysis of about 500 plant macrofossils from the new megafossil locality revealed shoots, leaves, trunks and fructifications belonging to horsetails, seed ferns, cycads, ginkgophytes, conifers and some taxa still to be classified as incertae sedis. So far, fern remains are missing from Bletterbach. Conifers dominate the fossil plant association, ginkgophytes are common, while pteridosperms, cycads and especially horsetails are rare in the flora.

4.1. Sphenophytes

A few sporophyll heads (4–6 mm in diameter) are hexagonal or much more rarely pentagonal; these could belong to the genus *Equisetites* (e.g., PAL 1395, Plate I, 1). Additional plant remains resemble horsetail leaf sheaths (40–70 mm wide and 20–38 mm high) with a smooth surface and pointed, subtriangular 'teeth' of max 11–14× 9–12 mm (e.g., PAL 1428, Plate I, 2).

4.2. Pteridosperms

At least two different leaf taxa have been determined as seed ferns.

A few small pinna fragments (up to 43 mm long and 23 mm wide) belong to the genus *Sphenopteris* (Brongniart) Sternberg, 1825. The inversely lanceolate pinnules (13×9 mm) are attached (sub) oppositely to oppositely to the rachis (e.g., PAL 1412, 1478, Plate I, 4, Plate IV, 5–6). The shape, dimensions and organization of the pinnules resemble these of *Sphenopteris suessii* Geinitz, 1869, described originally from the Collio Formation (early Permian) of the Trompia Valley in Italy (e.g., Sordelli, 1896; Remy and Remy, 1978).

Only two fragments belonging to the typical European Permian species, *Lepidopteris martinsii* (Germar in Kurtze) Townrow, 1960 have been found. The pinna fragments are up to 20 mm long and 7 mm wide. Pinnules are small (3.5–4 mm wide and 2 mm long), with an entire, decurrent margin (e.g., PAL 1017, Plate I, 7). They are closely and (sub) oppositely attached, without covering each other. No venation can be observed, apart from a trace of a midrib. Although the fragments are small and, thus, the intercalary pinnules are not visible, both the shape and the attachment of the pinnules to the rachis attribute these specimens to *L. martinsii*. That species has been recorded from e.g., the Marl Slate of England (Stoneley, 1958) and the Zechstein of Germany (e.g., Schweitzer, 1962; Poort and Kerp, 1990). Additionally, a dispersed ovuliferous disc belongs to *Peltaspermum* Harris, 1937 (e.g., PAL 1036, Plate I, 3). The ovuliferous disc has a diameter of 21 mm and is divided into 14 lobes. The lobes are deeply incised, 7–8 mm long and 2.5 mm wide, with a rounded apex. This ovuliferous disc might have belonged to the same plant as *L. martinsii*. Poort and Kerp (1990) recorded finding associated *Peltaspermum* discs and foliage in Germany, England and Italy (cuticle horizon of Bletterbach-Butterloch).

Fig. 2. Stratigraphic column of the Gröden Sandstone with the main fossiliferous horizons indicated.

4.3. Putative cycadophytes

At least two different types of leaves belong to the Cycadophytes. *Taeniopteris* sp. 1 is characterized by simple, elongated, entire-margined leaf fragments (max. 120 mm long and 21 mm wide) with the lamina inserted on the upper part of the rachis (e.g., PAL 870, Plate I, 5, Plate IV, 1). Lateral veins arise almost perpendicularly and show no bifurcations. The specimens resemble *Lesleya* (al. *Taeniopteris*) cf. *eckhardtii* Germar in Kurtze, 1839, apart from the almost perpendicular angle at which the veins arise from a stout rachis. Typical *Lesleya eckhardtii*, regularly found in Zechstein of Germany (Kerp, pers. comm., 2010) with secondary veins arising at an acute angle, has not been found so far in the newly discovered flora.

Taeniopteris sp. 2 has much broader entire-margined leaf fragments (60 mm long and 70–90 mm wide) with a strong rachis (e.g., PAL 844, Plate I, 6). The lateral veins arise at a slightly acuter angle then bend outwards and reach the margin almost perpendicularly. The two species differ mostly in the size of the leaves.

4.4. Ginkgophytes

Three different ginkgoalean leaf types (one only tentatively identified) can be distinguished in the new flora. Type 1 is a simple bifurcated leaf of about 60–80 mm length and 20–30 mm width. Generally, the leaves bifurcate only once at the basis (e.g., PAL 861, Plate I, 8). Each segment has an inversely- lanceolate shape with a rounded apex. Occasionally, each of the two segments bifurcates once more distally (e.g., PAL 1445, Plate I, 9). The veins are delicate and parallel; the preservation makes a counting of the veins difficult. This type can be assigned to the genus *Sphenobaiera* Florin 1936. In the ginkgophyte leaves the cuticles (PAL 933, Plate IV, 2; PAL 931, Plate IV, 8) are exceptionally well preserved.

Type 2 is characterized by c. 100 mm long and 70 mm wide, more wedge-shaped leaves. The petiole can be 20–25 mm long and 4–5 mm wide. The lamina bifurcates immediately at the base of the leaf; each segment bifurcates at least once more but sometimes more often. In the most complete specimen (PAL 2061, Plate I, 10) in the end seven individual segments can be counted, each being about 10–12 mm in width. Unfortunately, no complete leaf is preserved, the apex is always missing. The veins are distinct, up to eight are present in one of the segments (e.g., PAL 2061, Plate I, 10). This type slightly resembles *Sphenobaiera digitata* (Brongniart) Florin, 1936, although the leaves in the new material seem to be larger, the segments much broader and have more veins. Detailed macromorphological and cuticular analyses will enable to understand if these specimens can be assigned to *S. digitata*. Because of the wedge-shaped lamina, arising rather abruptly from the petiole (e.g., PAL 1436, Plate II, 1), this type 2 might belong to the genus *Baiera* Braun, 1843.

Type 3 comprises up to 75 mm long and 70 mm wide leaf fragments. The leaves are characterized by a partly monopodial and partly dichotomous structure (e.g., PAL 928, Plate II, 7). The segments are up to 40 mm long and 14 mm broad. Some seem to stem from bifurcations, some are definitively oppositely arranged on the rachis. Another specimen (e.g., PAL 1468, Plate II, 2) also shows some suboppositely arranged segments with a very large apical extension (70 mm long and 18 mm wide). The apex is rounded; no venation is visible. Because of the partly monopodial structure we cannot be sure that this type of leaf is assignable to the Ginkgoales.

4.5. Conifers

Several conifer shoot and leaf types can be distinguished in the Bletterbach flora. They are the dominant elements of this flora, e.g., *Ortiseia leonardii* Florin, 1964, which is the most common conifer. Large specimens (up to 20 cm long and 25 cm wide) have been found. Each lateral shoot fragment is up to 140 mm long and 40–45 mm wide. Lateral shoot fragments are up to 16–23 mm long and 3–5.5 mm wide, helically arranged, sessile, oval leaves are very common (e.g., PAL 1100, Plate II, 3, IV, 4). So far macroremains of *O. leonardii* have been recorded only from Cuecenes (Seceda, type locality) and Bletterbach (both Dolomites), while recently cuticles belonging to *O. leonardii* have been reported from the German Zechstein of Gera (Bödige, 2007). Macroremains of a second *Ortiseia* species, *O. visscheri* Clement-Westerhof, 1984, have been found so far only in the new macrofossil locality, but in much smaller numbers and only as ultimate shoot fragments. This latter species differs from *O. leonardii* in size (the leaves are smaller) and in having leaves that are much more adpressed to the axis than in *O. leonardii* where they stand out. One of the best specimens is PAL 839 (Plate II, 10), a 76 mm long and up to 15 mm wide shoot fragment.

Two types of conifer shoots with more needle-like leaves occur in the new megafossil locality. The first type is rather common but only as shoot fragments (up to 30 mm long and 20 mm wide). The axis is densely covered with slightly decurrent, helically arranged leaves with a pointed apex, that are 9–15 mm long and 1–2.5 mm wide (e.g., PAL 2019, Plate II, 9). Some of the shoot fragments show heterophylly (e.g., PAL 821, Plate III, 1). This leaf type can be identified as *Pseudovoltzia liebeana* (Geinitz) Florin, 1927, a conifer well known from the Zechstein (e.g., Schweitzer, 1963, 1968; Clement-Westerhof, 1988).

The second type is more rare and characterized by more elongated, narrow leaves (35–40×1.5–2 mm) with rounded apices (e.g., PAL 951, Plate III, 2). This type might represent the genus *Quadrocladus* Mädler, 1957, but this still has to be confirmed by cuticle analysis. *Quadrocladus* was already recorded from the Bletterbach gorge by Clement-Westerhof (1984) and Uhl and Kerp (2005).

The last type of conifer shoot is distinguished by small, helically arranged, adpressed leaves with rounded apices. The almost triangular leaves are 2–4 mm long and 1–2 mm broad. This type is very rare in the flora (e.g., PAL 822, Plate III, 4). As long as cuticular analyses are missing, this taxon is tentatively referred to the fossil genus *Pagiophyllum* Heer, 1881.

4.6. Cones

Several female and male cones have been found. The most common female cones are up to 60 mm long and 22 mm wide (e.g., PAL 866, Plate II, 5). The most abundant male cone fragments are up to 85 mm long and 24–30 mm broad (e.g., PAL 2034, Plate III, 3). Similar cones were assigned by Clement-Westerhof (1984) to *Ortiseia leonardii*. In some cases even *in situ Nuskoisporites* sp. has been found (e.g., PAL 344; Plate IV, 3).

Moreover, there are several other types of male and female cones that need a more detailed study (e.g., PAL 1422, Plate III, 6; PAL 1096, Plate II, 8). Only future detailed analyses will enable to attribute them to any of the known conifer taxa if it is possible to extract *in situ* pollen.

4.7. Incertae sedis

In the new Bletterbach flora some taxa have been distinguished, that could so far not been attributed to any group or genus.

One type is characterized by strap-like, elongated leaves, sometimes showing a bifurcation (e.g., PAL 858, Plate II, 6). These strap-like leaves may cover entire bedding planes (e.g., PAL 2014, Plate II, 4). They closely resemble the genus *Dicranophyllum* Grand'Eury, 1877, which has been recorded from e.g., the Carboniferous and early Permian of France and Germany. The affinity of *Dicranophyllum* is not yet clear; some suggest that it is an early Ginkgophyte (Taylor et al., 2009), whereas others consider *Dicranophyllum* to be a coniferophyte (Barthel et al., 1998; Rothwell et al., 2005). Apart from *Dicranophyllum*, another, completely different group of plants displays a slightly similar type of leaves, the

Czekanowskiales, an enigmatic group of gymnosperm plants, only known so far from the Mesozoic (Harris and Miller, 1974).

Some valve-like structures found in the Bletterbach assemblage are not assignable to any genus or group. They are 12–14 mm long and 10–13 mm wide, and characterized by a clear rim (about 1 mm wide) around the margin and 8–12 radiating ribs spreading from the attachment area to the inner margin of the rim (e.g., PAL 1448, Plate III, 5; PAL 1464, Plate III, 7). No group of plants from the Permian is known to possess such valve-like structures. However, the Mesozoic Czekanowskiales have female fructifications (*Leptostrobus*) consisting of an axis with loosely and spirally arranged bivalved capsules (Harris and Miller, 1974). These are smaller (max. 5 mm long and 5 mm broad) but show the same basic gross morphology.

4.8. Wood and charcoal

Several fragments of petrified and partially petrified wood have been found in the Bletterbach area, although not recorded from the new horizon. Most specimens are between 60 and 150 mm long and between 45 and 80 mm in diameter. One single stem fragment is even larger but it is strongly compressed. It is 40 cm long and over 50 cm wide and about 7 cm thick and half-way up a primary shoot is going off. The stem consists of a carbonized outer and a permineralized inner part (PAL 825, Plate III, 9).

Several small fragments of charcoal/fusain were found in the new locality (for more details see Uhl et al., 2012). The fragments are up to 46 mm long, 34 mm wide and 15 mm high (e.g., PAL 928, Plate III, 8).

5. Discussion

The newly discovered flora from the Bletterbach gorge is the first well-preserved and diversified flora from the late Permian of the Southern Alps. Until now the record was limited to well-preserved but fragmentary shoot and reproductive remains from the "cuticle horizons" of the Bletterbach Gorge, or a few badly preserved conifer shoot fragments and petrified wood remains e.g., from Neumarkt/Egna), Sinich/Sinigo (Aspmair and Krainer, 1998; Fritz and Krainer, 2006) and Mölten/Meltina (Aspmair, 1998; Fritz and Krainer, 1999).

Visscher et al. (2001) in their overview on the Permian floras from the Southern Alps stated that well-preserved plant fossils are rare in the Gröden Sandstone and that the main constituents of the flora from the Gröden Sandstone of the Bletterbach Gorge are conifer genera such as *Ortiseia*, *Majonica*, *Dolomitia* and *Pseudovoltzia*, rather than *Walchia*, *Ullmannia* and *Voltzia*. Although they clearly indicated that the various conifer taxa described by Clement-Westerhof (1984,

Plate I. Scale bar = 1 cm.

1. *Equisetites* sp., sporophyll heads (PAL1395).
2. *Equisetites* sp., horsetail leaf sheath (PAL 1428).
3. *Peltaspermum* sp., ovuliferous organ (PAL 1036).
4. *Sphenopteris* sp., frond fragment (PAL 1412).
5. *Taeniopteris* sp. 1, leaf fragment (PAL 870).
6. *Taeniopteris* sp. 2, leaf fragment (PAL 844).
7. *Lepidopteris martinsii* (Germar in Kurtze) Townrow, 1960, pinna fragment (PAL1017).
8. Ginkgophyte type 1, leaf fragment (PAL 861).
9. Ginkgophyte type 1, leaf fragment (PAL 1445).
10. Ginkgophyte type 2, leaf fragment (PAL 2061).

Plate II. Scale bar = 1 cm. *(see on page 8)*

1. Ginkgophyte type 2, leaf fragment (PAL 1436).
2. Ginkgophyte type 3, leaf fragment (PAL 1468).
3. *Ortiseia leonardii* Florin, 1964, shoot fragment (PAL 1100).
4. Incertae sedis, strap-like, elongated leaves (PAL 2014).
5. Female conifer cone (PAL 866).
6. Incertae sedis, strap-like, elongated leaves (PAL 858).
7. Ginkgophyte type 3, leaf fragment (PAL 928).
8. Male conifer cone (PAL 1096).
9. *Pseudovoltzia liebeana* (Geinitz) Florin, 1927, shoot fragment (PAL 2019).
10. *Ortiseia visscheri* Clement-Westerhof, 1984, shoot fragment (PAL 839).

Plate III. Scale bar = 1 cm. *(see on page 9)*

1. *Pseudovoltzia liebeana* (Geinitz) Florin, 1927, shoot fragment (PAL 821).
2. cf. *Quadrocladus* sp., shoot fragment (PAL 951).
3. Male conifer cone (PAL 2034).
4. *Pagiophyllum* sp., shoot fragment (PAL 822).
5. Incertae sedis, valve-like structures (PAL 1448).
6. Female conifer cone (PAL 1422).
7. Incertae sedis, valve-like structures (PAL 1464).
8. Charcoal fragments (PAL 928).
9. Permineralized wood fragments (PAL 825).

Plate IV. Scale bar = 50 μm. *(see on page 10)*

1. *Taeniopteris* sp. 1, cuticle (PAL 870)
2. Ginkgophyte type 1, cuticle (PAL 933)
3. *Nuskoisporites* sp. found *in situ* (PAL 344)
4. *Ortiseia leonardii*, cuticle (BUT 26)
5. *Sphenopteris sp.*, cuticle (PAL 1478)
6. *Sphenopteris* sp., cuticle (PAL 1412)
7. *Pseudovoltzia liebeana* (Geinitz) Florin, 1927, cuticle (PAL 865)
8. Ginkgophyte type 1, cuticle (PAL 931).

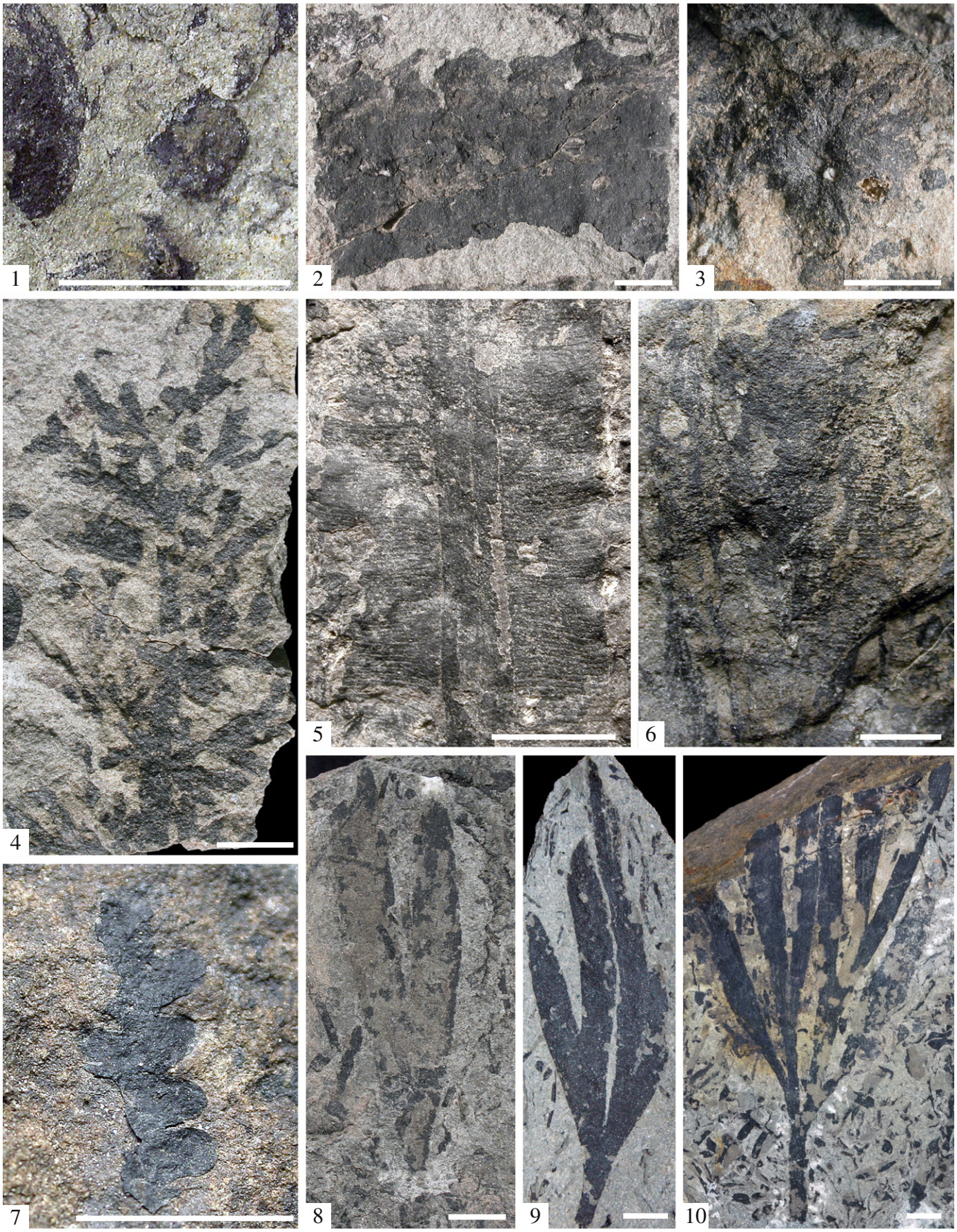


Plate I.

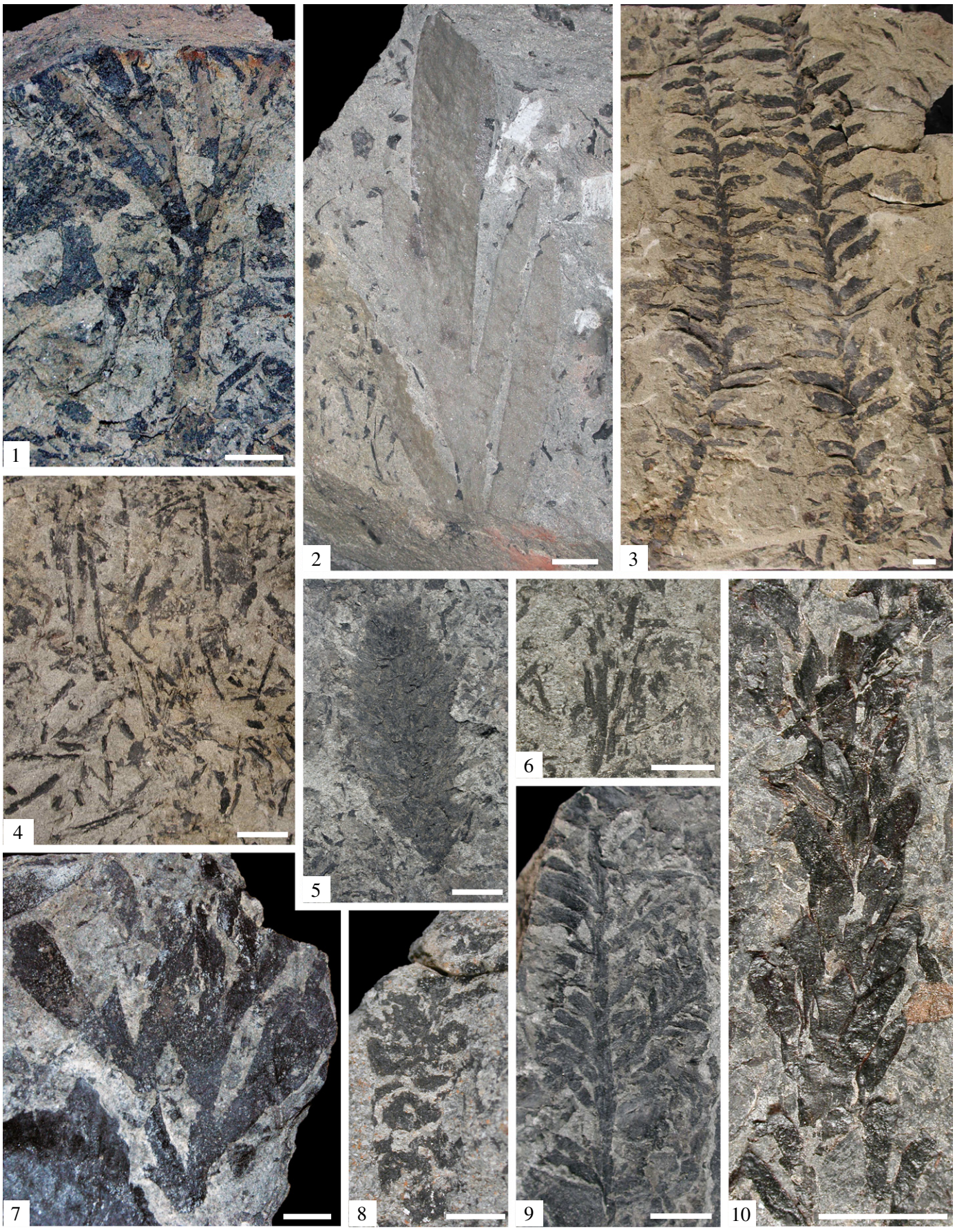


Plate II (*caption on page 6*).

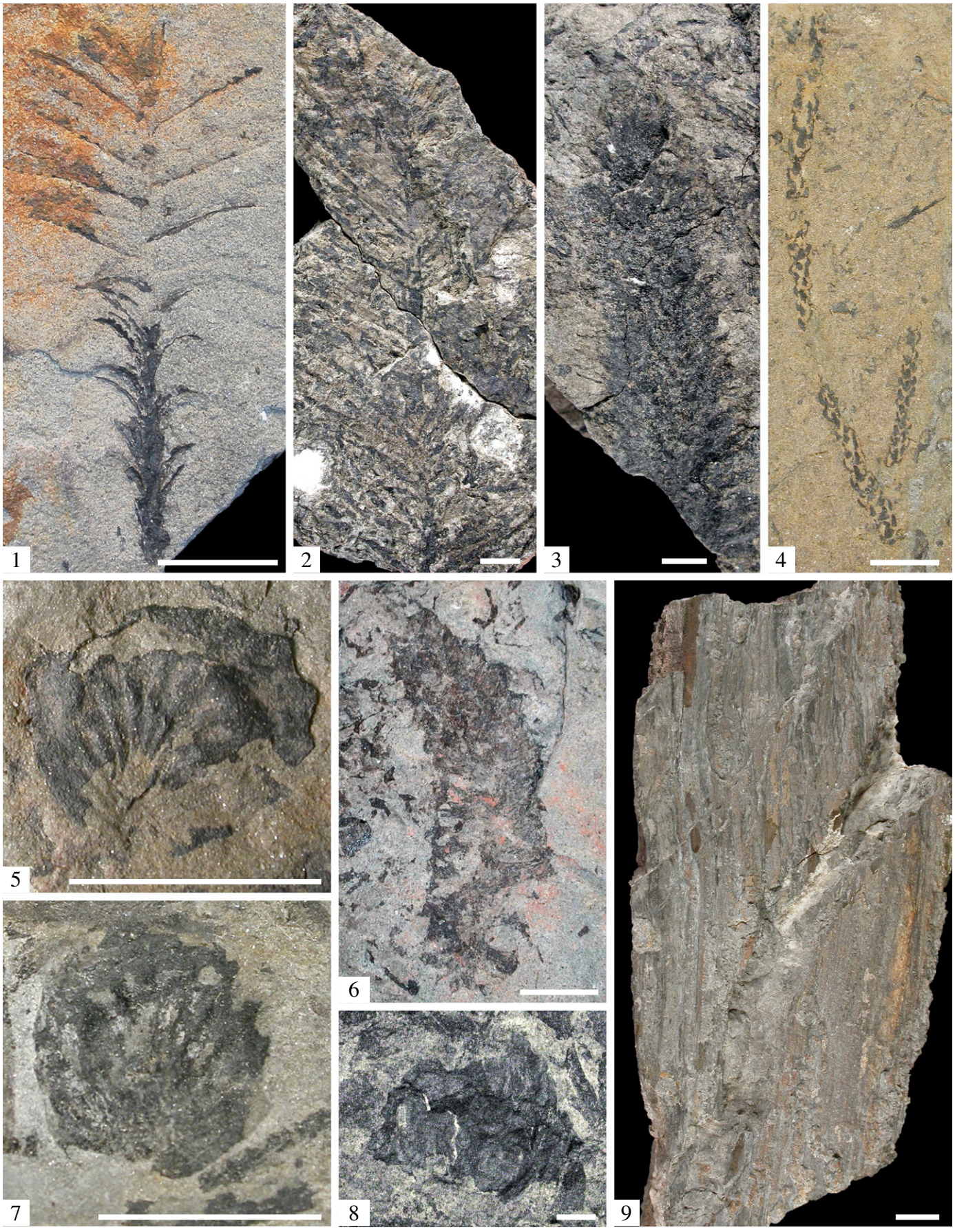


Plate III (*caption on page 6*).

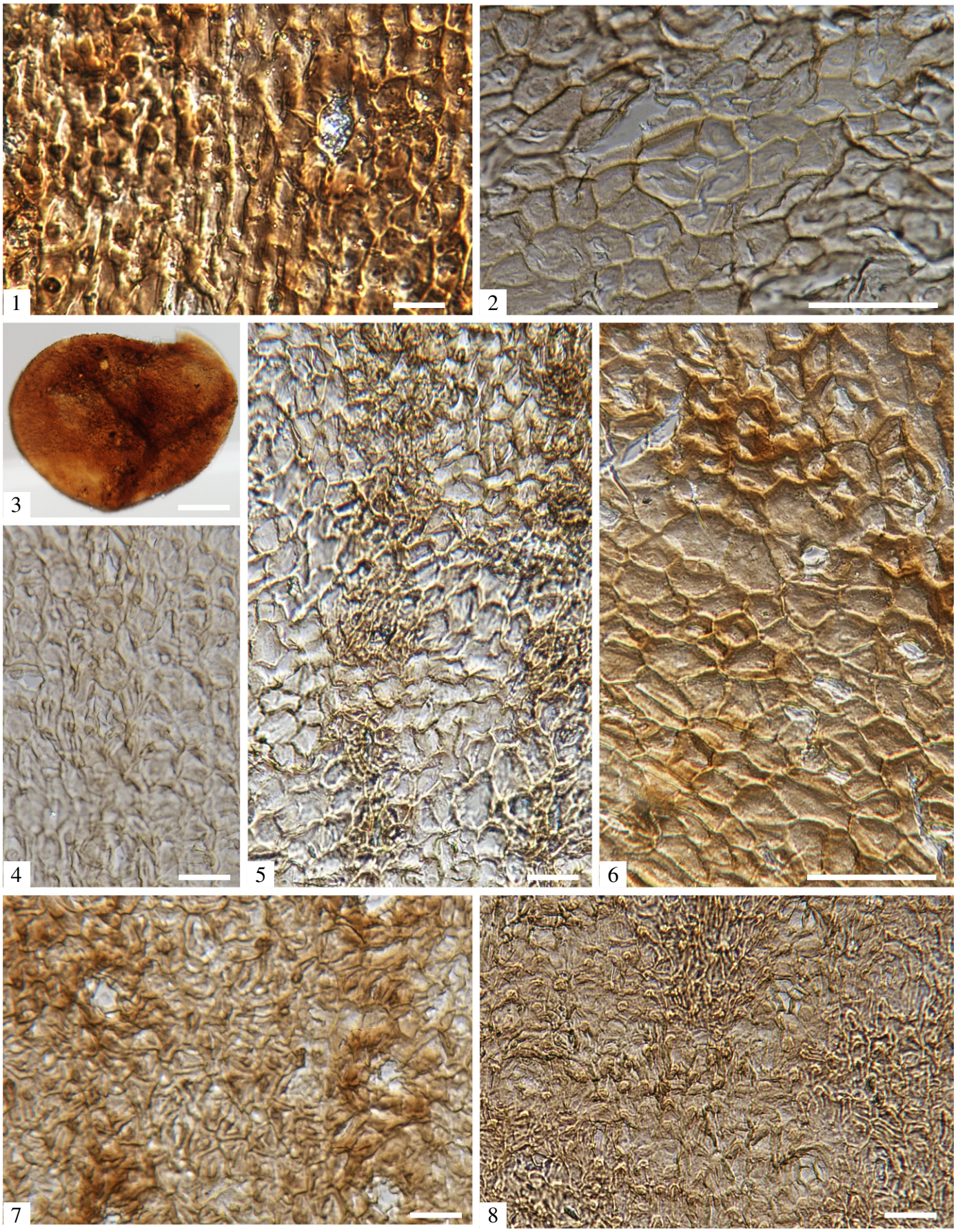


Plate IV (*caption on page 6*).

Table 1
Taxa currently recognized from the new megafossil locality and the cuticle horizons of the Bletterbach area.

State of preservation/nature of material	Clement-Westerhof (1984, 1986, 1987)	Poort and Kerp (1990)	Visscher et al. (2001)	Uhl and Kerp (2005)	This paper	Remarks
	Dispersed cuticles	Dispersed cuticles	Dispersed cuticles	Dispersed cuticles	Macrofossils	
Seed ferns						
Lepidopteris (=*Callipteris*) *martinsii*	x				x	*Lepidopteris* (=*Callipteris*) *martinsii*
Peltaspermum martinsii		x	x			*Lepidopteris martinsii*+*Peltaspermum* sp.
Peltaspermum sp.					x	
Sphenopteris suessii					x	
Sphenopteris sp.	x					
Ginkgophytes						
Sphenobaiera type 1					x	
Sphenobaiera type 2					x	
Sphenobaiera type 3					x	
Sphenobaiera sp.	x				x	
Cycadophytes						
Taeniopteris sp. 1					x	
Taeniopteris sp. 2					x	
Conifers						
Dolomitia cittertiae	x		x			
Majonica alpina	x		x			
Ortiseia leonardii	x		x		x	
Ortiseia visscheri	x		x		x	
Pagiophyllum sp.					x	
Pseudovoltzia liebeana	x		x		x	
Quadrocladus sp.	x			x	x	
Incertae sedis						
"Dicranophyllum"					x	
Bivalved structure					x	
Permineralized wood					x	
Charcoal					x	

1986, 1987) and the seed fern described by Poort and Kerp (1990) were only a part of the flora, as also evidenced by palynological assemblages (e.g., Klaus, 1963; Massari et al., 1994; Pittau, 2005), no other large floral remains were described so far. The discovery of a diversified flora with well-preserved cuticles (see Plate IV) in the Bletterbach area is thus of great importance. It contributes towards a much better understanding and more realistic reconstructions of the plant taxa that, to date, are known mostly from dispersed cuticles of bulk-macerated sediment samples.

An overview of the taxa currently recognized from the new megafossil locality and the cuticle horizons of the Bletterbach Gorge is presented in Table 1. Reports of taxa that have previously been reported from the Bletterbach area but that cannot be confirmed are summarized in Table 2. These include all reports of lycophyte remains as mentioned by Perwanger (1946) and Leonardi (1948, 1951, 1968), which were probably only unidentified conifer shoots or could belong to "*Dicranophyllum*".

Although identifications are still tentative, this new flora demonstrates that the vegetation in present-day southern Europe was more diverse during the late Permian than was known before. Apart from several conifer taxa, also callipterids, sphenopterids, taeniopterids and ginkgophytes are represented in the new flora. Except of callipterids, none of these forms have previously been reported from the Bletterbach area. Particularly, the occurrence of large ginkgophyte specimens is of great interest, because only few dispersed cuticles had been discovered to date and none of them have been published. The nearly complete ginkgophyte leaves from the new locality are among the best ginkgophyte fossils currently known from the late Permian of Europe. A contribution on ginkgophyte leaves with seeds apparently attached from the new locality has already been published (Fischer et al., 2010). Also the rare taeniopterids are of interest, because they have not been reported before from the Bletterbach area, probably because the brittle cuticles do not survive in bulk maceration and small fragments are difficult to identify.

In addition, the new flora enables better comparisons with other coeval floras from other localities in the southern Europe, notably the Vicentinian Alps where also floras with good cuticle preservation have been recovered. Several taxa recorded as dispersed cuticles from

Table 2
Taxa that have previously been reported from the Bletterbach area but that cannot be confirmed by the present study.

	Perwanger (1946)	Leonardi (1948, 1951, 1968)	Current interpretation
Lycophytes			
"*Lepidodendron* Stengel"	x		Probably conifer shoots
Lepidodendron cf. *sternbergii* vel *Schizolepis permensis*		x	"*Dicranophyllum*"
Lepidodendron cf. *veltheimianum*		x	Unidentifiable defoliated conifer shoots
Wood of *Lepidodendron*		x	Permineralized wood
Conifers			
Lebachia (= *Walchia*) *laxifolia*		x	Conifer shoot indet.
Lebachia sp.		x	Conifer shoot indet.

the cuticle horizons in the Bletterbach Gorge have not yet been found as megafossils, i.e., *Ortiseia jonkeri*, etc. Some taxa described from the Vicentinian Alps have not yet been found in the Bletterbach area, neither as megafossil nor as dispersed cuticles, i.e. *Pseudovoltzia sjerpii*. The new material also offers a much better basis for comparisons with floras from other parts of Europe. Although the floras from the Zechstein Basin are also dominated by conifers, the conifer taxa that are dominant in the Southern Alps have not yet been recorded from the Zechstein Basin. Taxa being well represented in the Zechstein Basin such as *Ullmannia frumentaria*, *U. bronnii*, *Quadrocladus solmsii* and *Q. orobiformis* were so far not recorded as megafossils in the late Permian floras of southern Europe. Only detailed macromorphological studies, in situ pollen and cuticular analyses will enable to understand whether these taxa had a restricted paleogeograpical distribution.

6. Conclusions

The Bletterbach is famous for its abundance and high diversity of ichnofaunas consisting of tetrapod footprints and for the perfectly preserved cuticles of small twigs and leaves yielded by a mudstone horizon below and two immediately above the waterfall (the so called "cuticle horizons"). Not only well-preserved but also tens of centimetres long fossil plant fragments from the new megafossil locality were recovered; these yielded also cuticles and *in situ* pollen. The new flora shows a high diversity in taxa. Representatives of almost all groups (horsetails, seed ferns, cycads, ginkgophytes, and conifers) typical of the late Permian have been distinguished in the flora. The sphenophyte remains are few and badly preserved, in the seed ferns, on the other hand, at least two different leaf taxa have been distinguished (*Sphenopteris* sp., *Lepidopteris martinsii*) as well as some ovuliferous organs belonging to the genus *Peltaspermum*. Also some putative cycadophytes were identified, with two different species of *Taeniopteris*. Three different leaf-types were distinguished in the ginkgophytes. The conifers are the most abundant and diversified group, with *Ortiseia leonardii*, *Ortiseia visscheri*, *Pseudovoltzia liebeana*, *Quadrocladus* sp., *Pagiophyllum* sp. documented also by several different female and male cones. There are also plant remains of doubtful botanical attribution, such as strap-like, elongated leaves resembling the genus *Dicranophyllum*, valve-like structures resembling the *Leptostrobus*-type of female fructifications and some wood remains, both preserved as permineralized wood and as charcoal. Reports of lycophyte remains previously reported from the Bletterbach cannot be confirmed; these were probably badly preserved conifer shoots or *Dicranophyllum*-type of leaves. The sphenopterids and taeniopterids are here recorded for the first time from the Bletterbach, as well as megafossils of the species *Ortiseia jonkeri* and *Pseudovoltzia sjerpii*.

The new material also offers a much better basis for comparisons with floras from other parts of Europe, since late Permian floras are scarce throughout Europe and North America, and also still incompletely understood. Thus, a detailed study of the new Bletterbach flora will lead to a better understanding of the taxonomic assignment of the different plant remains of the Southern Alps, and thus also to a much better understanding of the late Permian floras in Europe.

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