The Lopingian (late Permian) flora from the Bletterbach Gorge in the Dolomites, Northern Italy: a review

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ABSTRACT

This paper reviews the plant macro- and microfossil (palynoflora) record from the upper Permian Bletterbach succession in the Dolomites, northeastern Italy, and provides a survey of evidence of plant-insect interactions from the same strata. Plant megafossils (including *in situ* pollen and charcoal) come from several stratigraphic horizons within the section, and include sphenophytes, seed ferns (*Sphenopteris*, *Germaropteris*, alethopterid pinnules), putative cycadophytes (*Taeniopteris*), ginkgophytes (*Baiera*, *Sphenobaiera*, other probable ginkgophyte remains) and conifers (*Ortiseia*, *Pseudovoltzia*, *Dolomitia, Majonica*, *Quadrocladus*). Fossils of uncertain botanical affinities include *Leptostrobus*-like ovuliferous capsules, permineralised wood and charcoal. Specimens initially interpreted as lycophytes are regarded as inconclusive. Bletterbach plants displaying evidence of insect herbivory indicate an herbivory level of 1.95%, which is low in comparison to other Permian floras worldwide, but perhaps attributable to taphonomic bias. Plant-insect interactions preserved in the Bletterbach flora are dominated by external foliage feeding, followed by oviposition and galling, and exhibit rare presence of seed predation and wood boring. The maximum number of insect associations for a single Bletterbach plant was found on the conifer *Pseudovoltzia liebeana*, which displays four, mostly generalized associations. Based on approximately contemporary insect faunas in Europe, it is likely that the Bletterbach flora was consumed by a diverse assemblage of insect herbivores. Large monosaccate, taeniate bisaccate, monolete bisaccate and alete bisaccate pollen grains are the dominant forms in palynological samples, whereas spores are rare (<5%). Diverse assemblages of pollen grains and spores indicate that the late Permian flora must have included many taxa, such as several lycophytes, which presently have not been documented from allochtonous macrofossils. In summary, the different lines of fossil evidence indicate that the Bletterbach flora ranges among the most diverse and complex of Lopingian floras from Euramerica.

KEY WORDS

plant fossil assemblages, insect herbivory; palynomorphs, Wuchiapingian, UNESCO World Heritage Site, Dolomites

INTRODUCTION

Documented evidence of late Permian (Lopingian) plant fossils from Central Europe is relatively rare. Our current understanding of the plants and vegetation that were present in Europe during this significant geological period prior to the Permo–Triassic mass extinction event stems from fossils discovered from the Zechstein Basin, which extended from England toward the West to Poland and the Baltic region in the East and Germany to the South. The record of late Permian plants from southern Europe is even more under-reported, and thus comparisons of the vegetation in southern and northern Europe have not been possible to age date.

The plant fossils from the spectacular Bletterbach Gorge on the western edge of the Dolomites Region in northeastern Italy therefore are of special relevance to our understanding of Permian plant diversity in Europe. In recognition of this relevance, the Bletterbach Gorge has been included in the UNESCO

World Heritage Site DOLOMITES in 2009. Plant fossil assemblages from the Bletterbach sequence usually consist of small, highly fragmented compressions and dispersed cuticle material (Clement-Westerhof, 1984, 1986, 1987; Poort & Kerp, 1990). However, more recent and systematic fieldwork connected with a research project under the auspices of the Museum of Nature South Tyrol and Geoparc Bletterbach, and two subsequent research projects, unearthed several new fossiliferous horizons in the Bletterbach section. One of these sections included a bed located below a marine transgressive horizon that yielded comparatively large and well-preserved megafossils. Smaller plant fragments and dispersed cuticles originate from another bed directly above this marine horizon. Several hundred specimens were collected from these beds in the years 2003 through 2011 and subsequently were described and illustrated in series of scientific publications.

This contribution provides a synopsis of the Bletterbach flora, herein focusing on results obtained from newly collected material. A noteworthy aspect of these results is that the new material in several instances provided decisive clues in the linking of megafloral taxa with microfloral remains (i.e. palynomorphs) and/or dispersed cuticles, thereby enabling the reconstruction of whole-plant taxa. The new plant fossils demonstrate that sphenopsids, ferns, sphenopterid foliage, peltasperms, putative cycadophytes, ginkgophytes and conifers were constituents of the Bletterbach flora (e.g., Fischer et al., 2010; Uhl et al., 2012; Kustatscher et al., 2012, 2014, 2017; Bauer et al., 2014). The Bletterbach flora represents one of the most diverse, late Permian plant fossil assemblages in the Euramerican floral realm, far more diverse than previously thought.

2. HISTORICAL CONTEXT

The first mention of late Permian plant fossils from northern Italy is found in Gümbel (1877), who reported on the presence of '*Voltzia hungarica*, *Baiera digitata*, *Ullmannia bronnii*, *U. geinitzii*, *Carpolithes*, *Calamites* or *Equisetites*' and a fern fragment from the Gröden/Val Gardena Sandstone near Neumarkt/Egna (note that all geological and geographical terms referring to strata and places in northern Italy are given first in German and then in Italian). The first direct reference to plant fossils from exposures in the Bletterbach Gorge was published by Perwanger in 1946, who mentioned several well-preserved specimens, including a specimen he believed represented a *Lepidodendron* stem fragment. Leonardi built on these earlier studies, and described and figured several fossil tree trunks and axes from the Bletterbach area (Leonardi, 1948, 1950, 1951, 1952, 1953, 1955, 1957, 1968). He identified these specimens as '*Lepidodendron* cf. *sternbergii* Lindley et Hutton vel *Schizolepis permensis* Heer; *Lepidodendron* cf. *veltheimianum* St., *Lepidodendron* sp., *Lebachia* (=*Walchia* Auct.) *laxifolia* Florin and *Lebachia* (?) sp.'. Recent studies have demonstrated that the axis fragments with rhomboidal leaf scars previously identified as *Lepidodendron* in fact represent defoliated conifer twigs (Kustatscher et al., 2012).

Until recently, research on Bletterbach fossils focused on small compression fossils and cuticles. Although cuticle fragments obtained from Bletterbach sediments generally are small, they are abundant and the epidermal anatomy mostly is exquisitely preserved. A new conifer family, the Majonicaceae, and several new genera and species were erected based on vegetative remains, such as leaves and ultimate shoots, and reproductive organs, principally ovuliferous dwarf shoots and polliniferous cones, from cuticle-rich beds in the Bletterbach Gorge. This new conifer family included the taxa *Ortiseia visscheri* Clement-Westerhof, 1984, *O. jonkeri* Clement-Westerhof, 1984, *Pseudovoltzia sjerpii* Clement-Westerhof, 1987, *Majonica alpina* Clement-Westerhof, 1987 and *Dolomitia cittertiae* Clement-Westerhof, 1987. *In situ* pollen was used to determine that *Nuskoisporites dulhuntyi* Potonié et Klaus, 1954 is the prepollen of *Ortiseia* Florin, 1964, and that *Lueckisporites* Potonié et Klaus, 1954 is the pollen of *Majonica alpina* Clement-Westerhof, 1987 (Clement-Westerhof, 1984, 1986, 1987). Detailed morphological and ultrastructural analysis of *N. dulhuntyi* indicate that these large palynomorphs represent so-called prepollen, primitive pollen grains that lack a pollen tube to provide nutrition (haustorial) or serve as a device in the transfer of the gametes into the archegonium (Poort et al., 1997). Poort and Kerp (1990) described the foliage and ovuliferous discs of the seed fern *Peltaspermum martinsii* (Germar) Poort et Kerp, 1990, a taxon later transferred to the genus *Germaropteris* (Kustatscher et al., 2014). Palynological analyses of sediments from the Gröden/Val Gardena Sandstone and the Bellerophon Formation of the Bletterbach (Klaus, 1963) have attracted the interest of other palynologists. The detailed palynostratigraphical analysis of 25 fossiliferous levels by Pittau (in Massari et al., 1988, 1994, 1999) resulted in the identification of >100 palynomorph taxa indicative of a diverse, gymnosperm-dominated flora.

3. GEOLOGICAL SETTING

The Bletterbach Gorge is located at the western edge of the Dolomites Region, between the villages of Aldein/Aldino and Radein/Redagno (Fig. 1). The basalmost rocks in the gorge are andesites, rhyolitic lavas and ignimbrites of the Auer/Ora Formation, the uppermost formation of the Athesian Volcanic Group (Morelli et al., 2007). The volcanic rocks belong to a mega-caldera-system, which had its centre near Bozen/Bolzano and whose activity is dated from 284.9 ± 1.6 to 274.1 ± 1.4 million years ago, occurring during the end of the Sakmarian Stage and into the Kungurian Stage (Bargossi et al., 2007; Avanzini et al., 2007; Marocchi et al., 2008). The volcanic succession ranges up to 2000 m thick and was deposited during several, separate volcaniclastic events (Morelli et al., 2007).

The Permian volcanites are overlain by the ~210 m thick sedimentary succession of the Gröden/Val Gardena Sandstone, equivalent in German nomenclature to the Grödner Sandstein and in Italian to the Arenaria di Val Gardena. The unit was initially described as Grödner Sandstein by Richthofen in 1860. The boundary between the Athesian Volcanic Group and the Gröden/Val Gardena Sandstone occurs as an unconformity which resulted from a long period of subaerial erosion (Morelli et al., 2007), interrupted by a sedimentary hiatus of ~14–27 million years (Cassinis et al., 1999; Morelli et al., 2007). The base of the Gröden/Val Gardena Sandstone overlying the volcanites is characterized by poorly sorted conglomerates, pebbly and muddy sandstones and siltstones (Massari et al., 1988; Kustatscher et al., 2012, 2016). Towards the top of the stratigraphic succession are alternations of red to greyish fluvial siliciclastics, evaporites and mixed carbonate-siliciclastic deposits, reflecting environments that include alluvial fans, braided rivers, shallow channels, coastal sabkhas, evaporitic lagoons and shallow marine shelf deposits (Italian IGCP 203, 1986; Ori, 1988). Gypsum

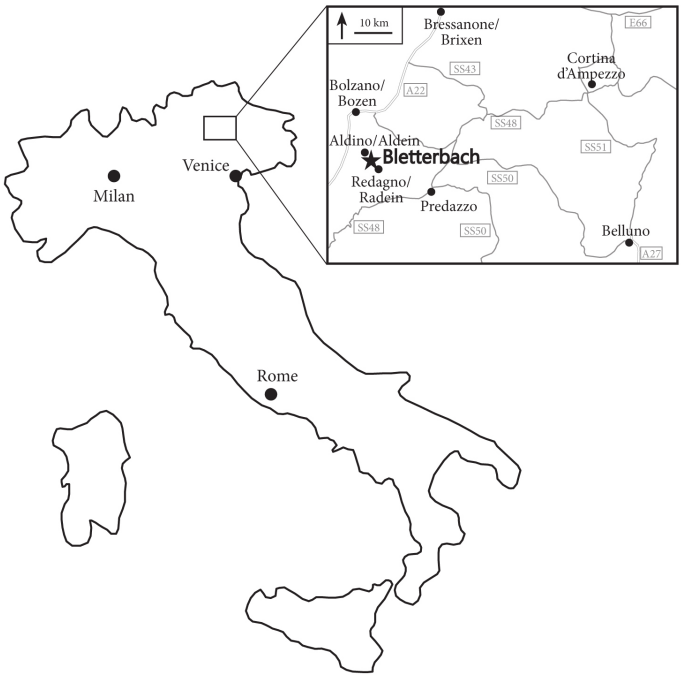

FIG. 1: Geographic position of the Bletterbach.

occurs occasionally in the red mudstone as sparse nodules or continuous layers interpreted as episodes dominated by continental sabkhas (Massari et al., 1988). Paleosols are represented locally by calcic soils and gypsic horizons with vertic features (Wopfner & Farrokh, 1988), suggesting a warm to hot, semi-arid to dry-subhumid climate with pronounced seasonality (Cassinis et al., 1999). At about 80 m from the base of the Gröden/Val Gardena Sandstone, a marine transgression is marked by a change in sediment colour from red to grey to muted hues of black that culminates in a prominently developed marine bed (Cassinis et al., 1999) containing a cephalopod fauna with *Stearoceras* sp. (Broglio Loriga et al., 1988; Prinoth, this volume). This marine horizon, called Cephalopod Bank (see also Prinoth, this volume), consists of a more erosion-resistant limestone; it represents the stratal impediment that causes the 'Butterloch' waterfall, so called because the structure, viewed from the top of the waterfall, resembles a 'Butterfass' or churn. Grey to blackish mudstones are exposed above the waterfall. Cross-bedded, shallow channel deposits and immature paleosols (entisols) represent the return to terrestrial conditions.

The transition from the Gröden/Val Gardena Sandstone to the overlying Bellerophon Formation is portrayed as an interfingering of fluvial and coastal–lagoonal deposits (Massari et al., 1988, 1994, 1999). The Bellerophon Formation is composed of dolomicrites rich in evaporitic gypsum ('*facies fiemmazza*' auct., Massari et al., 1988, 1994; Neri & Massari in Massari et al., 1999). The uppermost portion of the Bellerophon Formation is distinctly transgressive and overlain by oolitic grainstones, which correspond to the lower part of the Tesero Horizon, the lowermost member of the Werfen Formation, within which the P-Tr-boundary is located. The Bellerophon Formation is overlain by the lower Triassic Werfen Formation, a mixed carbonatic-siliciclastic succession, the upper Anisian Richthofen Conglomerate and a carbonate unit historically assigned to the Upper Sarl/Serla Dolomite, but probably belonging to the Contrin Formation (Piero Gianolla, Marco Avanzini, pers. comm., 2009–10) or to both (Rainer Brandner, pers. comm., 2017).

The Gröden/Val Gardena Sandstone is famous for its abundance and high diversity of tetrapod footprints (e.g., Conti et al., 1975, 1977, 1979; Ceoloni et al., 1988; Wopfner, 1999). Several horizons have yielded up to sixteen ichnotaxa belonging to various groups of tetrapods, including Gorgonopsia, Cynodontia, Lepidosauromorpha, Pareiasauridae and Rhynchosauroidea (Avanzini & Tomasoni, 2004). Plant megafossils occur at several levels in the Gröden/Val Gardena Sandstone (Fig. 2). Two mudstone horizons immediately above the Cephalopod Bank, about 80 m above the base of the Gröden/Val Gardena Sandstone, better known as 'cuticle horizons', contain small twigs and leaves with perfectly preserved cuticles (e.g., Clement-Westerhof, 1984, 1986, 1987; Poort & Kerp, 1990). Moreover, one narrow (>1 m thick) horizon below the waterfall consisting of medium- to coarse-grained greyish sandstones, sometimes with small, intercalated gypsum nodules is rich in large plant remains, and thus has been termed the 'megafossil horizon'.

The age of the Permian sedimentary succession of the Bletterbach Gorge is poorly constrained. Palynological data suggest a late Capitanian to Changhsingian (late middle to late Permian) age for the Gröden/Val Gardena Sandstone and the Bellerophon Formation (Massari et al., 1988, 1994, 1999; Pittau et al., 2005). However, typical Guadalupian (middle Permian) elements such as *Crucisaccites* Dyupina, 1970 are lacking, which would place the entire section in the Lopingian (late Permian). Cassinis and Ronchi (2001) and Posenato (2010) also suggested a Guadalupian age for part of the Gröden/Val Gardena Sandstone based on stratigraphic position. The tetrapod footprint fauna supports a Wuchiapingian age (early late Permian; Lucas & Hunt, 2006; Avanzini et al., 2011). All horizons rich in plant fossils occur above the first footprint level, and accordingly would also be within the Wuchiapingian (early late Permian). Moreover, the lower part of the overlying Bellerophon Formation is considered late Wuchiapingian in age (Ceoloni et al., 1988), which would place the Gröden/Val Gardena Sandstone within the Wuchiapingian. If the Cephalopod Bank can be correlated with the main Zechstein transgression (Kustatscher et al., 2017), then the Cephalopod Bank, and additionally the megafossil and cuticle horizons, would be middle Wuchiapingian in age.

4. MATERIAL AND METHODS

Fossils from the cuticle horizons mostly occur as small shoot and cone fragments that yield exceptionally well-preserved cuticles, while specimens (~500 specimens) from the megafossil horizon include long leaves up to 30 cm and branches with well-preserved cuticles, as well as polliniferous organs containing *in situ* pollen. This enables an association between the small leaf and shoot fragments recovered from bulk macerations and the megafossils, collected in the 1960s and 1970s and presently housed in the paleobotanical collections at Utrecht University, The Netherlands.

Cuticles were obtained from most specimens through maceration of small fragments in Schulze's reagent ($KClO_3$ and 30% HNO_3) and neutralised in ammonium hydroxide (NH_4OH, 5%). Moreover, bulk macerations were conducted to obtain large sample sets of cuticles that perhaps even include a few taxa not present in the macrofossil record. Samples were treated with HF (47%) for several days, sieved and then processed using the same procedure as for *in situ* material. Cuticles were mounted in glycerine jelly on microscope slides for light microscopic analysis

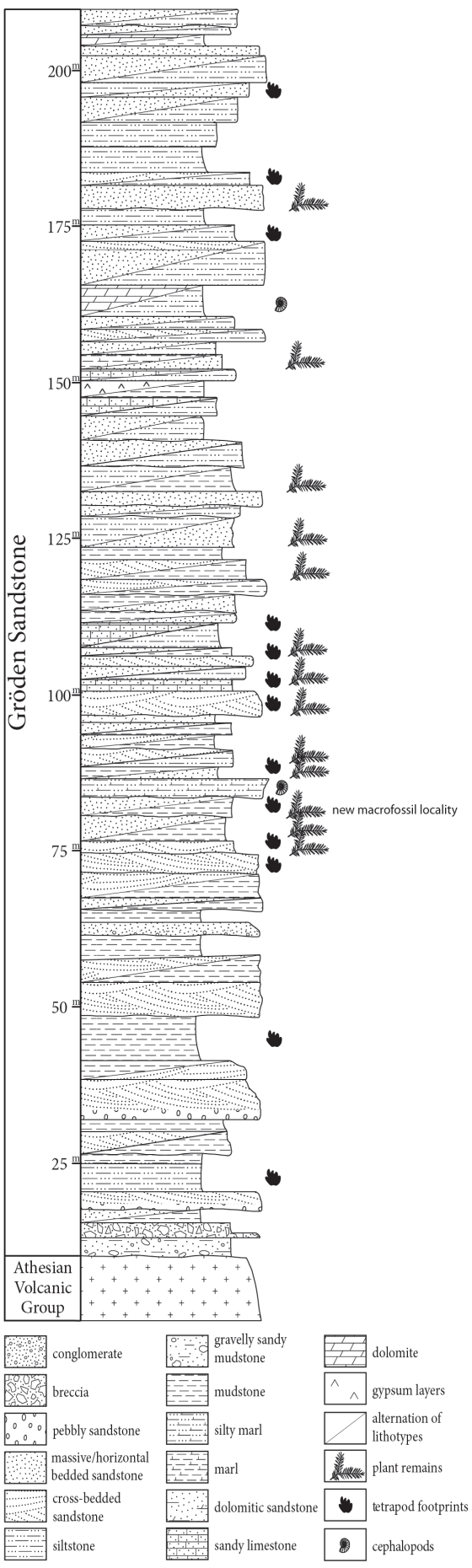

FIG. 2: Stratigraphic column of the Bletterbach succession with the main fossiliferous horizons indicated (mod. from Kustatscher et al., 2012).

and sealed with paraplast (see Kerp, 1990; Kerp & Krings, 1999; Batten, 1999). Hand specimens were photographed with a Canon Eos D550 digital camera according to procedures outlined by Kerp & Bomfleur (2011). Cuticle images were captured with a Nikon DS-5Mc digital camera attached to a Leitz Diaplan microscope and a Nikon DS-L2 control unit, and a Leica DM2500 with a Nikon DS-Fi1 Digital Camera and DS-L2 control unit.
Cuticle slides and megafossils from the megafossil horizon are stored at the Museum of Nature South Tyrol in Bozen/Bolzano (Italy) (specimen numbers preceded by 'PAL'). Specimens from the cuticle horizons with the prefix "UU" are from the collections of the Laboratory of Palaeobotany and Palynology, Utrecht University, The Netherlands.
Sediment samples for palynological analysis were mechnically crushed into small fragments and subsequently treated using standard techniques, including HCl and HF to dissolve carbonates and silicates (for details refer to Batten, 1999). The original slides of Klaus (1963) are housed at the Geologische Bundesanstalt of Austria in Vienna, subsequent slide collections are stored at the Universities of Cagliari, Sardinia (Pittau) and Utrecht (Visscher and co-workers).

5. MACROFLORA

Plant megafossils from the megafossil and cuticle horizons include leaves, shoots, branches, trunks, and reproductive organs of sphenophytes, seed ferns, putative cycadophytes, ginkgophytes and conifers. Compelling macrofossil evidence of ferns and lycophytes has not been produced to date. Ginkgophytes and conifers dominate the assemblage, whereas seed ferns, putative cycadophytes and especially sphenophytes are comparatively rare.

5.1. Sphenophytes

Sphenophytes are represented by a few axes and strobilus fragments (Kustatscher et al., 2014). The few sporophyll heads (4–6 mm in diameter) are hexagonal to pentagonal in shape and resemble the genus *Equisetites* Sternberg, 1833 (Plate 1a). A stem fragment with prominent ribs 2 mm wide, as well as several fragments of what appear to be leaf sheaths with pointed 'teeth' (11–14 x 9–12 mm) have also been found.

5.2. Seed ferns

At least four different leaf types have been assigned to seed ferns (see Kustatscher et al., 2014), The first leaf type, *Germaropteris martinsii* (Germar in Kurtze) Kustatscher et al., 2014, is one of the most common seed fern fossils in the Lopingian of Euramerica (Kustatscher et al., 2014). Several leaf fragments and ovuliferous organs of *G. martinsii* come from the megafossil horizon; cuticles have been recovered from the cuticle horizons. Pinnules (3.5–4 mm long and 1–2 mm wide, with a rounded apex) extend from a rachis that is often densely covered in large, blister-like swellings (Plate 1b, 4a); the venation is not normally visible due to the massive cuticle and a thick coaly layer representing the mesophyll. Partially macerated specimens show a pinnate venation (Poort & Kerp, 1990). Fronds are amphistomatic; stomatal complexes are irregularly scattered and consist of deeply sunken guard cells surrounded by 5–6 (rarely 7–8) subsidiary cells, each bearing a papilla that arches over the porus (Plate 5a, b). Epidermal cells are polygonal to isodiametric and bear a central papilla. *Peltaspermum*-type ovu-

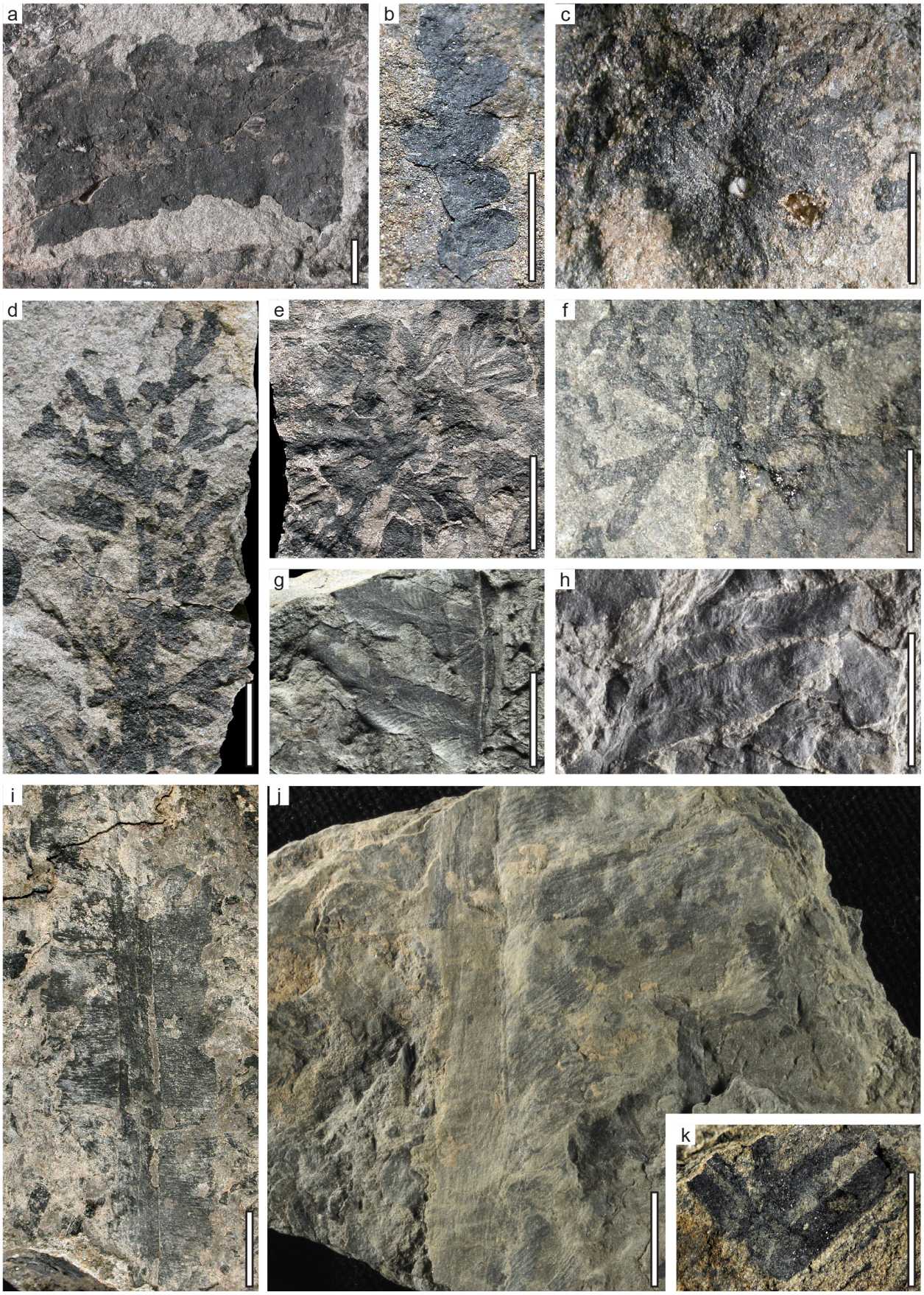

PLATE 1: Characteristic sphenophytes, seed ferns and putative ginkgophytes from the megafossil and cuticle horizons of the Bletterbach Gorge. Scale bar = 1 cm. **a.** Leaf sheet fragment of sphenophyte stem (PAL 1428), megafossil horizon; **b.** Leaf fragment of *Germaropteris martinsii* (Germar in Kurtze) Kustatscher et al., 2014 (PAL1017), megafossil horizon; **c.** Ovuliferous *Peltaspermum*-like disc of *Germaropteris martinsii* (Germar in Kurtze) Kustatscher et al., 2014 (PAL1036), megafossil horizon; **d.** Leaf fragment of *Sphenopteris suessii* Geinitz, 1869 (PAL1412), megafossil horizon; **e.** Leaf fragment of *Sphenopteris suessii* Geinitz, 1869 (PAL1408), megafossil horizon; **f.** Leaf fragment of *Sphenopteris* sp. (PAL1478), megafossil horizon; **g.** Pinnae fragment with alethopterid pinnules (UU 23779), cuticle horizon; **h.** Pinnae with alethopterid pinnules (UU 23761), cuticle horizon; **i.** Leaf fragment of *Taeniopteris* sp. A (PAL 870), megafossil horizon; **j.** Leaf fragment of *Taeniopteris* sp. B (UU BUT11), cuticle horizon; **k.** Apical leaf fragment of a cycadophyte-like leaf (PAL1003), megafossil horizon.

liferous discs (Plate 1c) believed to belong to the same plant as the *G. martinsii* leaves, are radially symmetrical, ca. 21 mm in diameter, with prominent ribs on the upper surface and up to 14 marginal, semi-circular lobes.

Two leaf types assignable to the genus *Sphenopteris* (Brongniart) Sternberg, 1825 have been reported from the megafossil horizon, although dispersed cuticles attributable to this genus have also been found in the cuticle horizons (Hans Kerp, pers. observ.). *Sphenopteris suessii* Geinitz, 1869, a taxon known exclusively from the Permian of the Alps region (Visscher et al., 2001), is characterized by inversely lanceolate pinnules (13 x 9 mm) with constricted bases that are attached (sub)oppositely to oppositely to the rachis (Plate 1d–e). The leaves are amphistomatic, with each of the isodiametric epidermal cells bearing small papillae. The slightly sunken stomata are scattered irregularly in what appear to be faintly differentiated intercostal fields with isodiametric cells. Stomatal complexes possess 4–5 subsidiary cells, some of which bear papillae that partially overarch the stomatal pit. The second form, *Sphenopteris* sp. (Plate 1f), is represented by a single fragment. Pinnules arise (sub-)alternately from the striate rachis (3 mm wide), are more or less irregularly dichotomous, and fork at least twice in their proximal aspect. Leaf segments are free; no veins are discernible. The leaves are amphistomatic and have a thin cuticle. The epidermis shows alternating stomata-free bands of isodiametric cells (veins?) and rows of stomata immersed in slightly smaller, isodiametric epidermal cells. The stomatal complexes are monocyclic, with deeply sunken guard cells and 5–8 isodiametric subsidiary cells, each bearing a massive papilla.

Pinnae with attached alethopterid pinnules (Plate 1g–h) are sometimes found in the cuticle horizons but rarely in the megafossil horizon. The pinnules (5–15 x 5–5.5 mm) are oblong to slightly falcate with a rounded apex and decurrent base, the latter which runs down along the axis and merges with the subjacent pinnule. The prominent midrib extends to 2/3 of the pinnule length; secondary veins are distinctive and fork once in the distal half of the lamina and, rarely, a second time near the midvein. The irregularly arranged epidermal cells are isodiametric to rectangular; some bear papillae or trichomes. Stomatal complexes are arranged in rows and have 5 (rarely 4 or 6) isodiametric subsidiary cells bearing small papillae.

5.3 Putative cycadophytes

At least two different types of strap-like leaves are tentatively assigned to cycadophytes (see Kustatscher et al., 2014). *Taeniopteris* sp. A is restricted to the megafossil horizon, while *Taeniopteris* sp. B also occurs in the cuticle horizons. *Taeniopteris* sp. A is characterized by simple, linear, entire-margined leaves up to 21 mm wide, with the lamina inserted at the upper portion of the prominent midvein (Plate 1i). Lateral veins extend from the midvein at almost a perpendicular angle and run unforked to the margin. The lateral veins usually are straight, but curve distally just before reaching the leaf lateral margin; 15–18 veins per centimetre reach the margin. The leaves are amphistomatic with slightly elongate epidermal cells that bear papillae. Stomatal complexes are scattered, guard cells are sunken and the 6–7 (rarely 8) isodiametric subsidiary cells bear solid papillae. The specimens resemble *Lesleya eckhardtii* Germar in Kurtze, 1839 from the German Zechstein but differ in having an almost perpendicular angle in which the veins arise from the stout midvein. *Taeniopteris* sp. B has much wider, entire-margined leaves (up to 90 mm wide) with a strong midvein (Plate 1j). Lateral veins arise at angles of 70°, arch slightly and reach the margin at angles of 80–90° with a density of 12–18 veins per cm. A few of the veins fork once close to the midvein. The leaf is amphistomatic and has thin cuticles. The isodiametric to elongate epidermal cells bear papillae or are thickened. Stomatal complexes are monocyclic, with sunken guard cells and 5–7 subsidiary cells bearing papillae.

A single leaf fragment has been recovered that is pinnate (Plate 1k), with incompletely preserved segments (6–17 x 2–4 mm) which arise at an angle of 40°. The fragmentary nature and poor preservation of the specimen (it lacks a cuticle) do not permit a precise assignment. Other segmented, cycad-like leaves have been attributed to *Pterophyllum* Brongniart, 1828, *Pseudoctenis* Seward, 1911 and *Plagiozamites* Zeiller, 1894 (e.g., Stoneley, 1958; Schweitzer, 1986; Pott et al., 2010). However, *Pterophyllum* recently has been redefined to accommodate bennettitalean foliage only (Pott et al., 2007a, 2007b); bennettitalean affinities cannot be demonstrated for any of the Paleozoic taxa.

5.4. Ginkgophytes

At least five different ginkgophyte leaf types have been described from the Bletterbach flora (for more details see Bauer at al., 2014). Ginkgophyte remains are mostly from the megafossil horizon; however, cuticle and smaller leaf fragments also have been found in the cuticle horizons (Bauer et al., 2014; Kustatscher et al., 2017). *Baiera digitata* (Brongniart) Heer, 1876 is the most abundant taxon, composed of leaf fragments (35–117 x 18–67 mm) that display the characteristic subdivision into petiole and lamina. The lamina is wedge-shaped, longer than wide, and subdivided into two symmetrical, primary segments. Each segment forks once or twice at about the same distance from the lamina base, thus resulting in a regular branching pattern. Each segment is linear to slightly elliptical or spindle-shaped, entire-margined, and has a somewhat convex apex. Up to eight parallel veins occur in the ultimate segments (Plate 2a).

Leaf fragments (60–90 x 20–40 mm) that lack a petiole have been assigned to *Sphenobaiera* sp. A (Bauer et al., 2014). These leaves (Plate 2b) fork once, close to the base and with a basal angle of 30–50°; each of the two segments is up to 12 mm wide and sometimes deeply incised. Segments are broadly lanceolate, reaching their largest width in the middle part, and the apex is convex or acute. Veins are delicate, occur in parallel fashion and bifurcate several times. In addition, a shoot segment with two leaves in organic connection originates from one of the cuticle-bearing stratigraphic horizons; these leaves are most likely of the *Sphenobaiera*-type (Bauer et al., 2014). Dispersed ovules/seeds that probably were produced by ginkgophytes also have been reported from Bletterbach Gorge. The seeds are roundish to ovoid in shape, up to 1.3 cm long and 1 cm wide (Fischer et al., 2010). Two of these seeds appear to be attached to *Baiera digitata*-type leaves. Although the ovules/seeds and leaves are not well preserved, their close association, together with a very similar epidermal anatomy, suggest that both were produced by the same plant (Fischer et al., 2010). The pattern in which the two organs co-occur resembles a phenotypic aberration documented in modern *Ginkgo biloba* L., 1771 from Japan that is known as *O-ha-tsuki* (Fuji, 1896; Fischer et al., 2010).

In addition to bona fide ginkgophyte remains, there are several foliage types that have been assigned tentatively to ginkgophytes (Bauer et al., 2014). The most frequent type occurs in the form of single-veined leaf fragments up to 5 mm wide and variable in length that fork once or twice (Plate 2f). The fragments

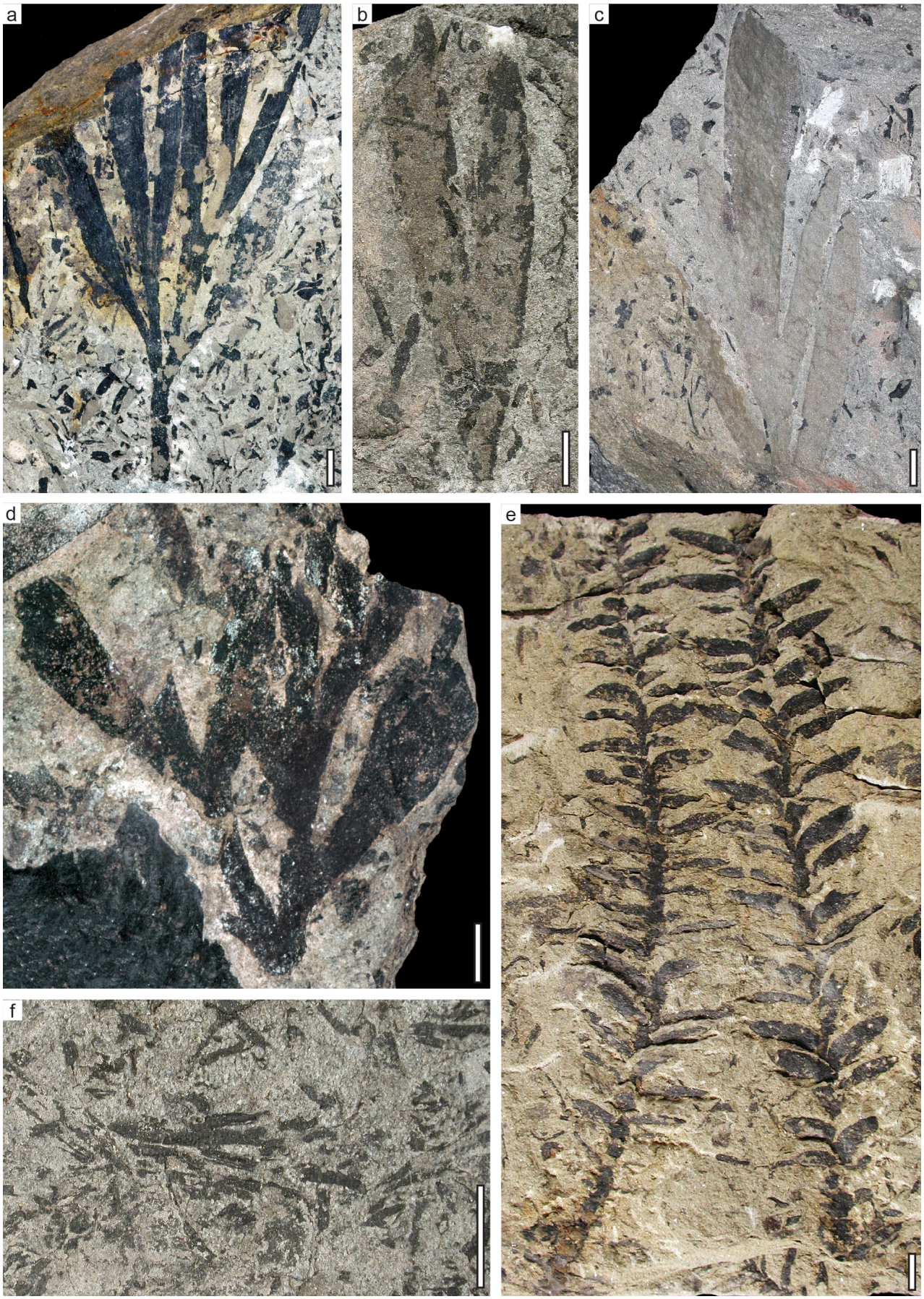

PLATE 2: Characteristic ginkgophytes and conifers from the megafossil and cuticle horizons of the Bletterbach Gorge. Scale bar = 1 cm. **a.** Complete leaf of *Baiera digitata* (Brongniart) Heer, 1876 (PAL2061), megafossil horizon; **b.** Simply dissected leaf of *Sphenobaiera* sp. A (PAL861), megafossil horizon. **c.** *Psygmophyllum*-like putative ginkgophytes (PAL1468), megafossil horizon; **d.** Putative ginkgophyte (PAL928), megafossil horizon. **e.** *Ortiseia leonardii* (Florin) Clement-Westerhof, 1984 (PAL 1100), megafossil horizon. **f.** *Dicranophyllum*-like leaf fragments (PAL858), megafossil horizon.

resemble the leaves of *Trichopitys* Saporta, 1875, *Polyspermophyllum* Archangelsky et Cúneo, 1990 and *Dicranophyllum* Grand'Eury, 1877, but also Czekanowskiales and conifers cannot be ruled out as possible source producers (see also 4.6). The second enigmatic foliage fossil is a large, more or less wedge-shaped leaf (Plate 2c) that is subdivided into five segments, the middle one of which is much larger than the others. The smaller, outer segments are more or less lanceolate and taper towards the tip, while the middle segments are oblanceolate and increase in width (up to 19 mm) towards the tip. Numerous tenuous, bifurcating veins are present. This leaf fragment differs from other late Paleozoic ginkgophyte leaves in the irregular subdivision of the lamina, but resembles certain members in the enigmatic genus *Psygmophyllum* Schimper, 1870. However, the leaf fragment differs from the latter in the shape of the individual leaf segments. The last foliage fossil (Plate 2d) tentatively attributed to the ginkgophytes is a multi-dissected leaf. The ultimate segments of this leaf are club-shaped, with a maximum width of 14 mm.

5.5. Conifers

Conifers are the dominant element in the cuticle horizons and provide an important component of the megafossil horizon. Eight species from five genera are known from Bletterbach Gorge. Consisting of three species, *Ortiseia leonardii* (Florin) Clement-Westerhof 1984, *O. visscheri* Clement-Westerhof, 1984, and *O. jonkeri* Clement-Westerhof 1984; the taxon *Ortiseia* Florin, 1964 is the most speciose conifer genus (Plate 3a-d, 4b–d).

Ortiseia leonardii is the most common conifer fossil in the megafossil assemblage. The ultimate branches are part of a plagiotropic, penultimate branching system. The leaves of the ultimate branches (6–15 x 4–7 mm) are helically arranged, non-decurrent, ovate, with a slightly constricted base and an acute to obtuse apex (Plate 2e, 3a). The leaves are amphistomatic, with stomatal complexes arranged in rows. Stomatal complexes are normally dicyclic with 4–6 papillate subsidiary cells and sunken guard cells (Plate 5c). The ovuliferous cone is compound, with helically arranged bract-ovuliferous dwarf shoot complexes. The dwarf shoots have numerous sterile scales and one adaxially positioned central sporophyll (Clement-Westerhof, 1984). *In situ* prepollen of *Nuskoisporites dulhuntyi* has been found in the pollen sacs of the polliniferous cones of all three *Ortiseia* species (Clement-Westerhof, 1984; Kustatscher, 2012). *Ortiseia leonardii* is common in the Southern Alps (Cuecenes, Bletterbach) and Vicentian Alps (Florin, 1964; Clement-Westerhof, 1984; Kustatscher et al., 2012), and constitutes a rare element in some exceptional German Kupferschiefer plant fossil assemblages (Gera: Bödige, 2007).

Ortiseia visscheri, is a less common conifer that so far has only been recorded for the Bletterbach Gorge (Clement-Westerhof, 1984), where it is represented by ultimate shoot fragments and isolated leaves (Plate 3b). The shoot morphology, reproductive organs and epidermal features of this taxon resemble *O. leonardii*, but *O. visscheri* has smaller leaves (ultimate leaves 5–10 x 3–4 mm) and slightly different epidermal features, including stomatal apparatuses characterized by 6–7 subsidiary cells. The ovuliferous dwarf shoots have fewer sterile scales than those of *O. leonardii* (Clement-Westerhof, 1984). *Ortiseia jonkeri* (Plate 3c–d, 4b, d), the third species within *Ortiseia* and restricted to the Southern Alps (Dolomites and Vicentian Alps), is known from several horizons at Bletterbach Gorge including the cuticle horizons, but apparently does not occur in the megafossil horizon. As in the other *Ortiseia* species, *O. jonkeri* branches are plagiotropic; however, they are less robust than those of the other two *Ortiseia* species. Moreover, the taxon has thinner axes, a different type of leaf attachment, smaller narrow-triangular to lanceolate leaves (leaves 2.5–5 x 1–1.5 mm), and differs slightly in epidermal features (Plate 5d–e). The ovuliferous dwarf shoots are smaller than those of the other two species, and they have larger numbers of sterile scales than *O. visscheri*.

The best-known genus in the Majonicaceae is *Pseudovoltzia* Florin, 1927. In the new megafossil horizon, *Pseudovoltzia liebeana* (Geinitz) Florin, 1927, a well-known species from Zechstein deposits in Germany and England (e.g., Schweitzer, 1963, 1968), is represented by foliated, ultimate shoot fragments as much as 30 cm long and isolated leaves. Leaves are helically arranged, decurrent, imbricated, strap-like, and possess pointed to obtuse apices (9–30 x 1–5 mm). Some of the shoots are heterophyllous and have leaves with variable lengths and shapes (e.g., Plate 3e, 3k). The leaves are amphistomatic, with the monocyclic stomatal complexes arranged in rows and generally surrounded by 6–7 subsidiary cells (Plate 5f). The dwarf shoots are symmetrical, with two lateral and one central sporophyll, as well as two intermediate sterile scales that are fused at the base (Clement-Westerhof, 1987, pl. 8, fig. 4). The principal differences between *P. liebeana* and the other species, *P. sjerpii* Clement-Westerhof, 1987, a taxon restricted to the Dolomites and the Vicentian Alps, are the shape of the dwarf shoot and central sporophyll, as well as the shorter, generally more ovate, leaves.

Majonica alpina Clement-Westerhof, 1987 (Plate 4f–h), present at Butterloch Gorge both in the megafossil and cuticle horizons, in the Vicentian Alps and the German Zechstein, has shoots with highly variable leaves with three different leaf types (for details, see Clement-Westerhof, 1987). Leaves possess a contracted leaf base and are helically arranged on the shoots, and extend from the axis straight or slightly diverging. The different leaf types were described ranging from narrow-triangular with an acute apex and straight margin (up to 35 x 6 mm), to ovate with an undulating margin and obtuse apex (10 x 4 mm). Leaves are amphistomatic, with monocyclic stomatal complexes (7–8 subsidiary cells) arranged in interrupted rows (Plate 5g). The dwarf shoots are stalked, with one to four fused central, sterile scales and two lateral sporophylls with ovule attachments near the base. *Majonica* seeds are single-winged; the *in situ* pollen grains belong to the dispersed taxon *Lueckisporites virkkiae*.

Dolomitia cittertiae Clement-Westerhof, 1987 (Plate 3f), formally described based on material from Bletterbach Gorge, also occurs in both the megafossil and the cuticle horizons. *Dolomitia* Clement-Westerhof, 1987 is heterophyllous with two leaf types, one of which is linear to lanceolate (up to 20 x 5 mm), while the other is ovate (up to 8 x 4 mm). Both leaf types are decurrent and possess an obtuse apex. The leaves are amphistomatic, monocyclic stomatal complexes with 7–9 subsidiary cells that are scattered or arranged in interrupted rows (Plate 5h). The dwarf shoots of *Dolomitia* bear a short stalk, two lateral and one central sporophyll, and thirteen triangular, sterile scales. Ovules, bracts and polliniferous cones of *Dolomitia* remain unknown (Clement-Westerhof, 1987).

The genus *Quadrocladus* Schweitzer 1960, originally described from the German Zechstein (Uhl & Kerp, 2005), is known both from the megafossil and cuticle horizons, but appears to be generally rare. The taxon is represented by isolated shoots and leaf fragments. The leaves are helically arranged, linear and straight (up to 40 x 1–3 mm) with rounded apices (Plate 3g, 5i). The

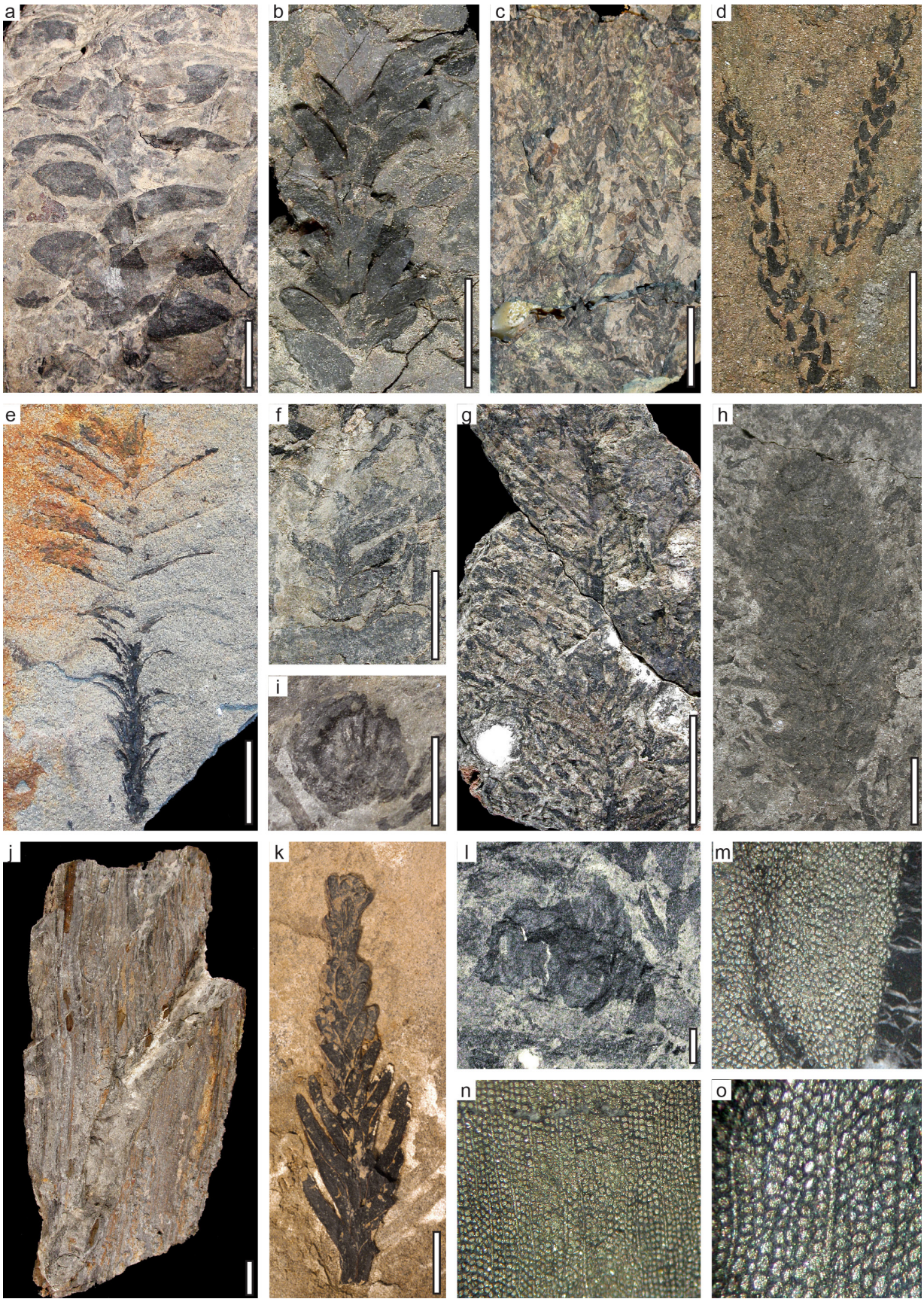

PLATE 3: Characteristic conifers from the megafossil and cuticle horizons of the Bletterbach. **a.** Ultimate shoot of *Ortiseia leonardii* (Florin) Clement-Westerhof, 1984 (UU14101), cuticle horizon; **b.** Ultimate shoot of *Ortiseia visscheri* Clement-Westerhof, 1984 (PAL859), megafossil horizon; **c.** Shoot of *Ortiseia jonkeri* Clement-Westerhof, 1984 (UU14110), cuticle horizon; **d.** Ultimate shoot of *Ortiseia jonkeri* Clement-Westerhof, 1984 (PAL822), megafossil horizon; **e.** Ultimate shoot of *Pseudovoltzia liebeana* (Geinitz) Florin, 1927 (PAL821), megafossil horizon; **f.** Ultimate shoot of *Dolomitia cittertiae* Clement-Westerhof, 1987 (PAL865), megafossil horizon; **g.** Shoot of *Quadrocladus* Schweitzer, 1960 (PAL 951), megafossil horizon; **h.** Unidentified ovuliferous conifer cone (PAL867), megafossil horizon; **i.** *Leptostrobus*-like valves (PAL1464), megafossil horizon; **j.** Permineralized wood (PAL 825), Bletterbach; **k.** Ultimate shoot of *Pseudovoltzia liebeana* (Geinitz) Florin, 1927 (??), cuticle horizon; **l.** Charcoal (PAL928), megafossil horizon; **m.** Detail of permineralized wood with cells partly filled by pyrite and partly compressed (PAL825), Bletterbach; **n.** Detail of permineralized wood with parenchym cells and rays (PAL825), Bletterbach; **o.** Detail of figure 30 with with parenchym cells and rays (PAL825), Bletterbach.

PLATE 4: Mesofossils after bulk maceration from the cuticle horizons. **a.** Leaf fragment of *Germaropteris martinsii* (Germar in Kurtze) Kustatscher et al., 2014; **b.** Shoot fragment of *Ortiseia jonkeri* Clement-Westerhof, 1987; **c.** Ovule/Seed fragment of *Ortiseia* sp.; **d.** Ovuliferous dwarf shoot of *Ortiseia jonkeri* Clement-Westerhof, 1987; **e.** Ovuliferous dwarf shoot of *Pseudovoltzia liebeana* (Geinitz) Florin, 1927 (arrows indicate the central and two lateral ovule attachment areas); **f.** Ovuliferous dwarf shoot of *Majonica alpina* Clement-Westerhof, 1987 (arrow indicates the attachment area); **g.** Ovuliferous dwarf shoot of *Majonica alpina* Clement-Westerhof, 1987; **h.** Single winged seed of *Majonica alpina* Clement-Westerhof, 1987

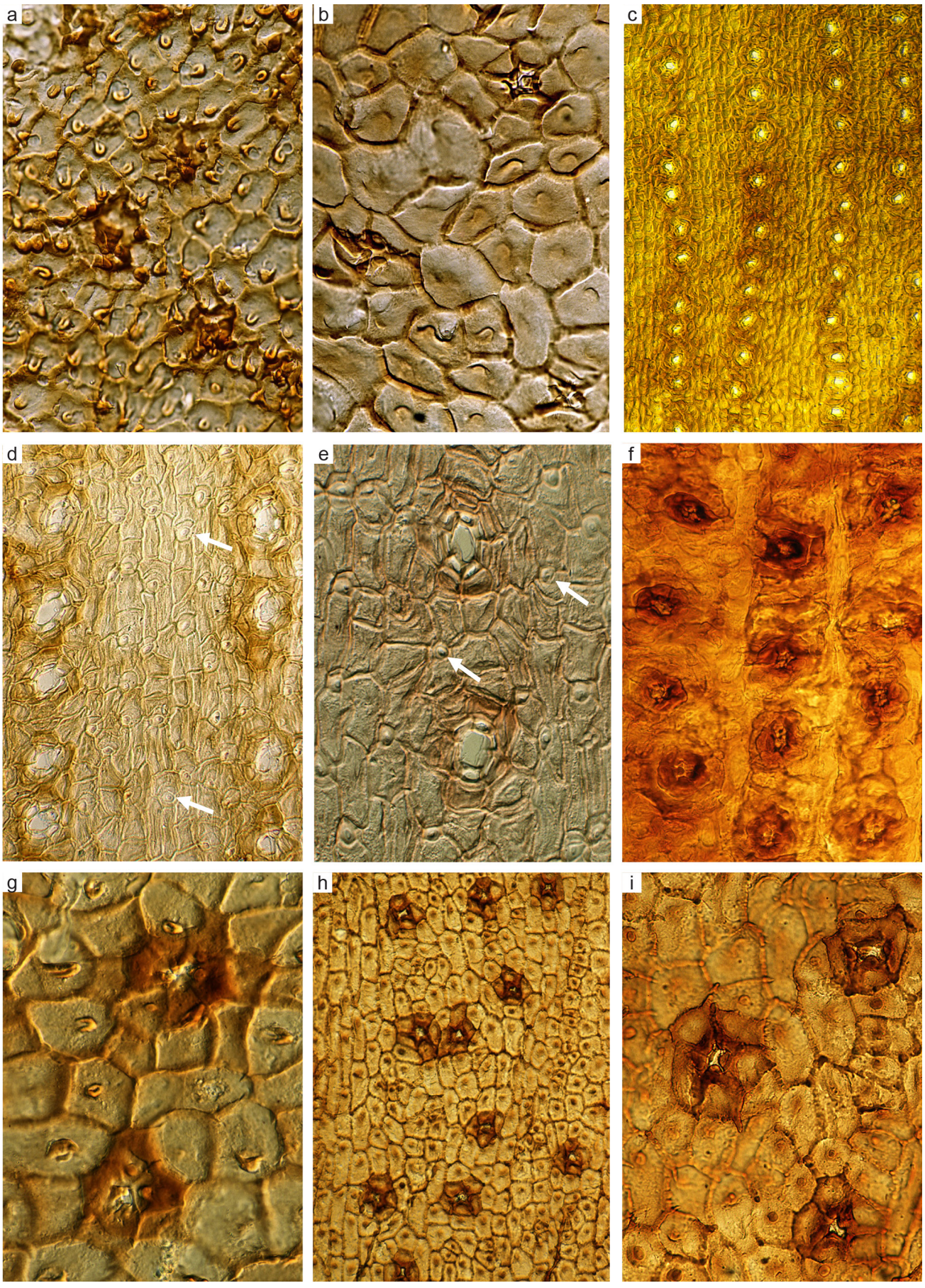

PLATE 5: Cuticles after bulk maceration from the cuticle horizons. **a.** *Germaropteris martinsii* (Germar in Kurtze) Kustatscher et al., 2014; **b.** *Germaropteris martinsii* (Germar in Kurtze) Kustatscher et al., 2014; **c.** *Ortiseia leonardii* (Florin) Clement-Westerhof, 1984; **d.** *Ortiseia jonkeri* Clement-Westerhof, 1984 (arrows indicate some of the hair bases); **e.** *Ortiseia jonkeri* Clement-Westerhof, 1984 (arrows indicate some of the hair bases); **f.** *Pseudovoltzia sjerpii* Clement-Westerhof, 1987; **g.** *Majonica alpina* Clement-Westerhof, 1987; **h.** *Dolomitia cittertiae* Clement-Westerhof, 1987; **i.** *Quadrocladus* Schweitzer, 1960 (PAL 951).

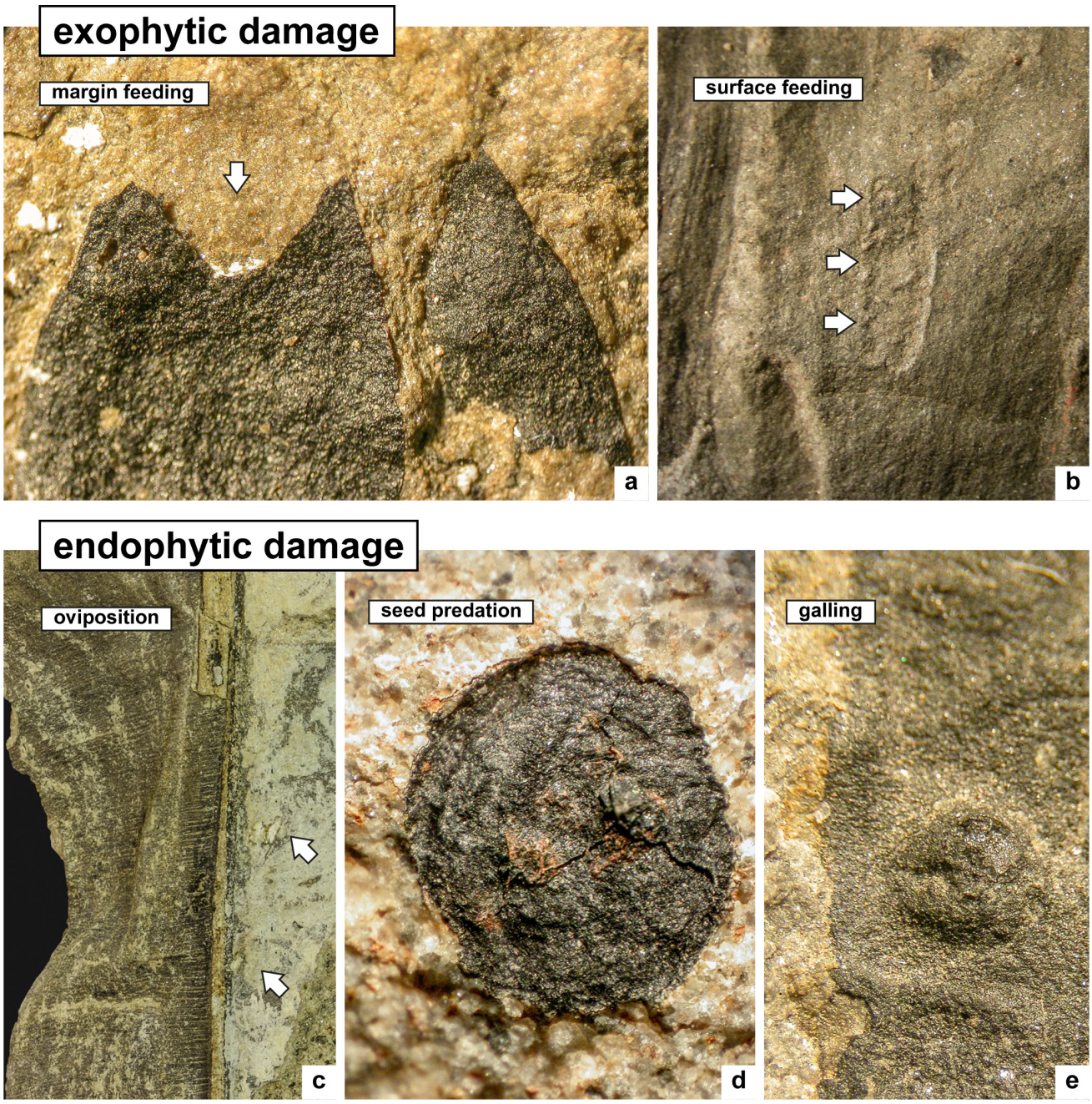

FIG. 3: Insect-mediated damage of leaves from the Bletterbach Gorge (Western Dolomites); **a.** Excision of leaf apex (DT13) on *Ortiseia leonardii* (PAL 2020); **b.** Window feeding with a distinct callus on an undetermined gingkophyte (PAL 1455); **c.** Insect interactions on a cycadophyte with oviposition on the midvein (DT76; white arrows); **d.** Seed predation (DT74) on PAL 1088; **e.** Woody spheroidal leaf gall on *Quadrocladus* sp. (PAL 1464).

leaves are amphistomatic, with stomatal complexes scattered or in short rows. Stomatal complexes are generally monocyclic, with on average 4–5 subsidiary cells, each bearing an inward pointing papilla. Several additional conifer reproductive structures have been recovered from the new megafossil horizon, but these specimens still need to be studied in detail and systematically assigned.

5.6. Incertae sedis, wood and charcoal

The Bletterbach macroflora has yielded several valve-like structures (12–14 x 10–13 mm) that are characterized by a distinct marginal rim (about 1 mm wide) and 8–12 radiating ribs emerging from the attachment area to the inner margin of the rim (Plate 3i) (Kustatscher et al., 2012). These structures are unknown in any of the plant groups recorded for the Permian, but are similar to the ovule-bearing organs of the Mesozoic Czekanowskiales (*Leptostrobus*) based on their construction of an axis around which are loosely and spirally arranged bivalved capsules (Harris et al., 1974). Several fragments of petrified and partially petrified wood have been found dispersed at Bletterbach Gorge. Most specimens have a carbonized outer and permineralized inner part (Plate 3j, 3m–o). Additionally, several charcoal fragments (Plate 3l), up to 46 x 34 x 15 mm in dimension, come from the megafossil horizon (see Uhl et al., 2012).

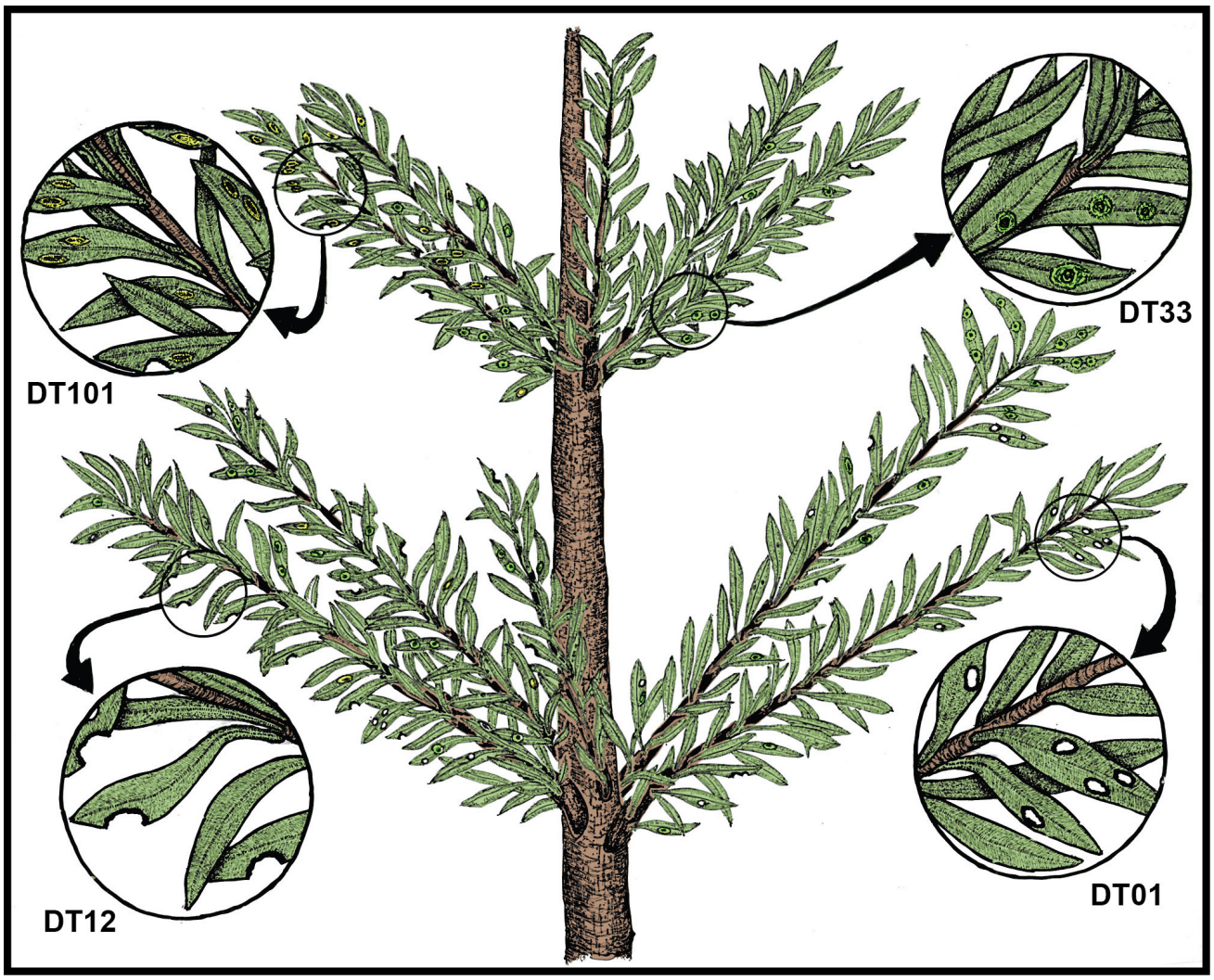

FIG. 4: The insect herbivore component community of the conifer *Pseudovoltzia liebeana*, from the Lopingian (Wuchiapingian) Gröden/Val Gardena Sandstone. Four DTs are represented on this host plant, including hole feeding (DT01), margin feeding (DT12), oviposition (DT101), and galling (DT33). Herbivore insect culprits responsible for these DTs likely were beetles (DT01), orthopteroids (DT12), sternorrhynchan hemipterans (DT33) and palaeodictyopteroids or polyphagan beetles (DT101) (from Labandeira et al., 2016)

6. PLANT-INSECT ASSOCIATIONS

The Bletterbach flora is relatively non-speciose floristically compared to other Permian floras in the Gondwanan floral realm, and similarly consists of a modest spectrum of insect damage. A rather modest bulk-floral level of 1.95% characterizes herbivory on the Bletterbach flora, based on 1531 censused foliage items (Labandeira et al., 2016). In terms of abundance, herbivory on the Bletterbach flora is dominated by external foliage feeding, especially margin feeding, represented by several damage types (= "DTs"), like shallow to deeper excisions of the leaf margin or apex feeding (Labandeira et al., 2016; Fig. 3). The abundance data indicate a dominance of generalized damage (79%), when compared to specialized damage (21%). By contrast, when analyzed by the diversity of the insect damage, the Bletterbach flora is dominated by specialized interactions (68.7%, N=11) such as galling, compared to generalized interactions (31.3%, N=5). A comparison of DT abundance data versus DT diversity data indicates that the specialized interactions are rare and distributed over a number of the plant taxa. The rather high degree of specialization in the Bletterbach flora is elevated in comparison to other Permian floras worldwide and also to Triassic floras in the same area of the Dolomites Region.

One particular measure of the extent of insect herbivory on the Bletterbach flora is an examination of the component community of herbivores on a particular plant. A component community consists of all trophically dependent herbivores (and their predators) on a particular host-plant species (Root, 1973). Notably, the conifer *Pseudovoltzia liebeana* (Fig. 4) exhibits the most diverse component community of herbivores in the Bletterbach flora, consisting of three external feeders – a margin feeder (DT12), a hole feeder (DT1) and an oviposition maker (DT101) – and a single internal feeder, the galler DT33 (Labandeira et al., 2016). This relative depauperate component community can be compared with analogous Middle Triassic (Anisian) seed fern *Scytophyllum bergeri* Bornemann, 1856 from the same region that exhibits an almost fourfold greater spectrum of DT diversity, including a broad variety of margin feeding, hole feeding, surface feeding, oviposition, piercing and sucking, galling and leaf mining. This increase in component community interactions may indicate a dramatic expansion of herbivory following the end-Permian ecological crisis (Wappler et al., 2015; Labandeira et al., 2016). In addition, there was a significantly greater expansion of herbivore partitioning of plant tissues during the Middle Triassic in the wake of the end-Permian ecological crisis. There probably is modest taphonomic loss of the Bletterbach

flora, and thus the bulk-floral herbivory level of 1.95% could be an under-representation. However, this value is commensurate, within a factor of two to three, with bulk-floral values from Euramerica and Gondwana (Plumstead, 1963; Adami-Rodrigues et al., 2004; Labandeira & Allen, 2007; Prevec et al., 2009; Schachat et al., 2014; 2015), suggesting that Permian bulk-floral levels of herbivory were globally lower than those of the Middle Triassic, as measured by ten floras of Anisian and Ladinian age in the Dolomites Region (Labandeira et al., 2016). When bulk herbivory levels are assessed in their totality, it appears that most Middle Triassic values range from four to seven times that of the Bletterbach Flora, a significant increase (Labandeira et al., 2016). In addition, qualitative assessments, including the extent of plant-host specificity is considerably greater for the Middle Triassic Dolomite floras than for the Bletterbach flora in the same region.

7. THE PALYNOFLORA

Pollen grains and spores are the most abundant, well-dispersed plant fossils in late Permian sediments of the Bletterbach section. They can be recovered in unlimited quantities from grey mudstone horizons of the Gröden/Val Gardena Sandstone and grey silty marls of the Bellerophon Formation. During his pioneer study of the Permian palynoflora of the Southern Alps, Klaus (1963) already had distinguished 55 different species of pollen grains and spores; 36 of these were treated as new taxa; of those, 18 were based on well-preserved type-specimens that originated from the Bletterbach section (Plates 6–7; after Draxler, 2010). Although subsequently some of the species established by Klaus (1963) appeared to be synonyms of earlier described forms, the palynological richness of the Bletterbach record accrued more than twice the previous number of palynomorphs through detailed palynostratigraphical analysis of 25 fossiliferous levels by Pittau (in Massari et al., 1988, 1994, 1999). These palynological assemblages are characterized by the dominance (90–99%) of saccate gymnospermous pollen. Commonly present, often in high frequencies, are large monosaccate forms (*Nuskoisporites dulhuntyi*), several taeniate bisaccate forms (mainly *Lueckisporites virkkiae* Potonié et Klaus, 1954, but also species of *Lunatisporites* Leschik, 1955), monolete bisaccate forms (*Jugasporites delasaucei* (Potonié et Klaus) Leschik, 1956, species of *Limitisporites* Leschik, 1956), and some alete bisaccate forms (*Klausipollenites schaubergeri* (Potonié et Klaus) Jansonius, 1962, species of *Alisporites* Daugherty, 1941, *Falcisporites* Leschik, 1956, *Paravesicaspora* Klaus, 1963 and *Vesicaspora* Schemel, 1951). Less consistently present is a wide variety of characteristic saccate pollen types assignable to *Strotersporites* Wilson, 1962, *Striatopodocarpites* Sedova, 1956, *Striatoabieites* Sedova, 1956, *Gardenasporites* Klaus, 1963, *Perisaccus* Naumova, 1953, *Playfordiaspora* Maheswari et Banerji, 1975, *Scheuringipollenites* Tiwari, 1973 and *Gigantosporites* Klaus, 1963. Non-saccate gymnosperm pollen is rare in the assemblages and consists of various species of *Vittatina* Sedova, 1956, *Ephedripites* Bolkhovitina, 1953, *Pretricolpipollenites* Danzé-Corsin et al., 1963 and *Cycadopites* Wodehouse, 1933. The proportional representation of fern spores such as *Osmundacidites* Couper, 1953, *Cyclogranisporites* Potonié et Kremp, 1954 and *Punctatisporites* Ibrahim, 1933, as well as lycophyte spores, principally *Densoisporites* Dettmann, 1963, *Lundbladispora* Balme, 1963 and *Kraeuselisporites* Leschik, 1955) is very limited (0–5%). More than 25 different fossil-fern spore species have been recognized.

Although many individual palynospecies may have stratigraphic ranges extending into the Guadalupian, the overall composition of Bletterbach assemblages matches the characteristic Lopingian palynoflora known from Permian sequences throughout Europe, such as the Zechstein Basin (e.g., Grebe & Schweitzer, 1962; Clarke, 1965; Visscher, 1971; Schaarschmidt, 1963; Fijałkowska, 1994), the 'Haselgebirge' evaporites of the Northern Calcareous Alps in Austria (Potonié & Klaus, 1954), and the terrestrial Balatonfelvidék Sandstone Formation and marine Dinnyés Dolomite Formation of the Transdanubian Central Range in northern Hungary (Góczán et al., 1987; Haas et al., 1988).

The remarkable richness of the Bletterbach palynological assemblages confirms that the coeval macrofloral record is particularly deficient in capturing regional floral diversity. While most megafossils are likely to represent plants growing in relatively close proximity to the site of deposition, the various pollen types were transported by wind and water activity from a wide range of environments including extrabasinal habitats unsuitable for megafossil preservation. Through the study of pollen found *in situ* in pollen-bearing cones, thus far only two commonly occurring pollen types could be affiliated with coniferous megafloral genera, namely the prepollen *Nuskoisporites* Potonié et Klaus, 1954 belonging to *Ortiseia* and *Lueckisporites* Potonié et Klaus, 1954 affiliated with *Majonica* (Clement-Westerhof, 1984; Poort et al., 1997). The large number of other distinctive saccate-pollen species may point to the existence of plant communities characterized by conifers and/or seed ferns still unknown from the macrofloral record of the Bletterbach section. This is well-exemplified by the common presence of *Jugasporites delasaucei*, a pollen species found *in situ* in cones of *Ullmannia frumentaria* (Schlotheim) Göppert 1850, a well-known conifer of the Lopingian megaflora of the German Zechstein deposits (Potonié & Schweitzer, 1960; Grebe & Schweitzer, 1962; Schweitzer, 1962), but not yet identified in the Dolomites Region. Similarly, the presence of various lycopsids can only be inferred from their microspore record. Alternatively, the common occurrence of various ginkgoalean mega- and mesofossil remains is not consistent with the rarity of monosulcate pollen (*Cycadopites* Wilson et Webster, 1946) or other pollen types assignable to the ginkgophytes.

Apart from pollen grains and spores, the Bletterbach assemblages occasionally include microscopic remains of algae and fungi. Of particular interest is the presence in the Bellerophon Formation of robust-walled, single cells and (branched) multicellular chains that can be referred to *Reduviasporonites* Wilson, 1962 (synonym *Tympanicysta* Balme, 1979). Fundamental controversy exists over the biological identity of these palynomorphs. On morphological and chemical grounds, they have been interpreted as remains of saprophytic or pathogenic fungi (Visscher & Brugman, 1988; Visscher et al., 1996, 2011; Elsik, 1999; Sephton et al., 2009). Alternatively, an algal interpretation is regularly advocated (Afonin et al., 2001; Foster et al., 2002; Spina et al., 2015), filamentous green algae of either Zygnematales or Trentepohliales being regarded as nearest living relatives. However, morphological comparisons with potential counterparts show that these microfossils display near-identity to specialized hyphae and hyphal aggregates (sclerotia) of modern soil-borne fungi, such as *Rhizoctonia*, which act as resting structures allowing the fungus to survive adverse conditions (Visscher et al., 2011).

It should be recognized that the analysis of *in situ* pollen has

PLATE 6: Type-specimens of sporomorph species described by Klaus for the first time from the Permian of the Southern Alps (from Draxler, 2010; courtesy Geologische Bundesanstalt, Vienna). **a.** *Converrucosisporites dejerseyi* Klaus 1963, 60 x 96 µm (GBA2010/013/0001); **b.** *Converrucosisporites eggeri* Klaus 1963, diameter 42 µm (GBA2010/013/0002); **c.** *Endosporites hexareticulatus* Klaus 1963, diameter 90µm (GBA2010/013/0007); **d.** *Perisaccus granulatus* Klaus 1963, diameter 70 µm (GBA2010/013/0010); **f.** *Illinites parvus* Klaus 1963, 42 x 33 µm (GBA2010/013/0015); **g.** *Illinites gamsi* Klaus 1963, 62 x 38 µm (GBA2010/013/0014); **h.** *Illinites pemphicus* Klaus 1963, 85 x 50 µm (GBA2010/013/0016); **i.** *Jugasporites paradelasaucei* Klaus 1963, 63 x 34 µm (GBA2010/013/0019); **j.** *Jugasporites lueckoides* Klaus 1963, 65 x 40 µm (GBA2010/013/0021); **k.** *Limitisporites parvus* Klaus 1963, 42 x 31 µm (GBA2010/013/0020); **l.** *Scutasporites unicus* Klaus 1963, 56 x 38 µm (GBA2010/013/0027); **m.** *Striatites angulistriatus* Klaus 1963, 43 x 36 µm (GBA2010/013/0065); **n.** *Gigantosporites hallstattensis* Klaus 1963, 150 x 100 µm (GBA2010/013/0029); **o.** *Gigantosporites aletoides* Klaus 1963, 125 x 90 µm (GBA2010/013/0035); **p.** *Gigantosporites illinoides* Klaus 1963, 135 x 94 µm (GBA2010/013/0037).

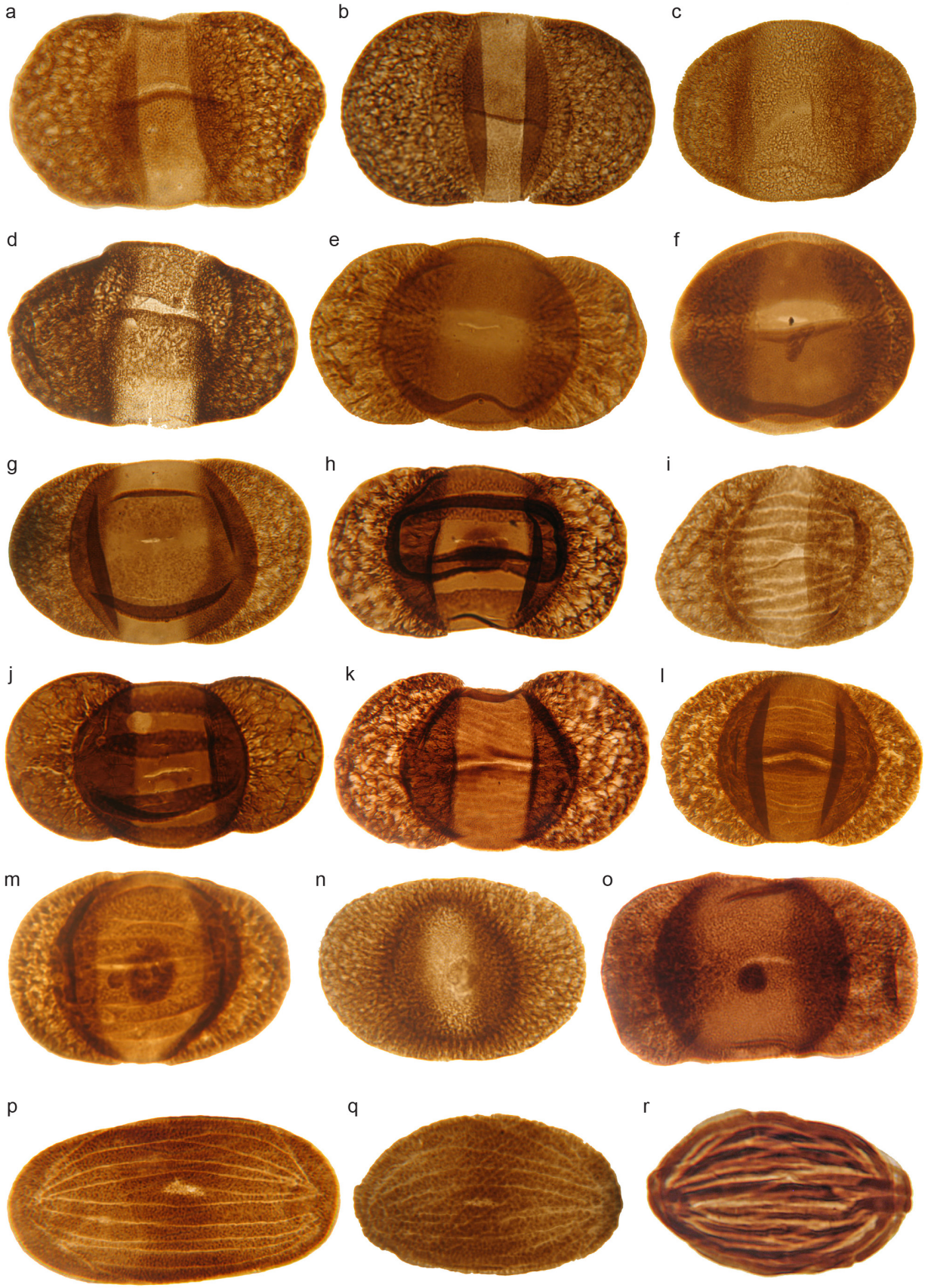

PLATE 7: Type-specimens of sporomorph species described by Klaus for the first time from the Permian of the Southern Alps (from Draxler, 2010; courtesy Geologische Bundesanstalt, Vienna). **a.** *Gardenasporites heisselii* Klaus 1963, 85 x 48 µm (GBA2010/013/0038). **b.** *Gardenasporites leonardii* Klaus 1963, 75 x 45 µm (GBA2010/013/0041). **c.** *Gardenasporites oberrauchii* Klaus 1963, 90 x 65 µm (GBA2010/013/0042). **d.** *Lueckisporites moroderi* Klaus 1963, 95 x 55 µm (GBA2010/013/0040). **e.** *Lueckisporites microgranulatus* Klaus 1963, 64 x 35 µm (GBA2010/013/0044). **f.** *Lueckisporites parvus* Klaus 1963, 50 x 45 µm (GBA2010/013/0048). **g.** *Lueckisporites globosus* Klaus 1963, 90 x 55 µm (GBA2010/013/0047). **h.** *Taeniaesporites ortisei* Klaus 1963, 90 x 45 µm (GBA2010/013/0051). **i.** *Striatites minor* Klaus 1963, 55 x 38 µm (GBA2010/013/0064). **j.** *Taeniaesporites labdacus* Klaus 1963, 95 x 45 µm (GBA2010/013/0054). **k.** *Stroterisporites jansonii* Klaus 1963, 150 x 90 µm (GBA2010/013/0058). **l.** *Stroterisporites wilsonii* Klaus 1963, 170 x 83 µm (GBA2010/013/0061). **m.** *Striatites marginalis* Klaus 1963, 74 x 48 µm (GBA2010/013/0063). **n.** *Vesicaspora schemelii* Klaus 1963, 50 x 34 µm (GBA2010/013/0064). **o.** *Limitisporites leschikii* Klaus 1963, 74 x 48 µm (GBA2010/013/0023). **p.** *Vittatina ovalis* Klaus 1963, 75 x 38 µm (GBA2010/013/0077); **q.** *Vittatina angulistriata* Klaus 1963, 72 x 40 µm (GBA2010/013/0078). **r.** *Ephedripites primus* Klaus 1963, 35 x 20 µm (GBA2010/013/0079).

demonstrated that the richness of Bletterbach palynological assemblages may be overestimated as a result of taxonomic oversplitting. The taxonomy of dispersed fossil pollen grains and spores largely is based on arbitrary morphological criteria, and in late Permian palynostratigraphy there has been a strong tendency to delimit narrowly defined form-species without considering the possibility of natural intraspecific variability. Nevertheless, particularly among saccate pollen, one may often observe gradual morphological transitions between palynospecies and even between palynogenera. Such transitions are characterized by continuous variation in size and shape of the body and the sacci, and the organization of proximal apertures (Visscher, 1971). *In situ* pollen already has presented a more natural concept of the species *Jugasporites delasaucei* and *Lueckisporites virkkiae*. The variability observed in *J. delasaucei* includes forms which frequently are referred to as species of *Limitisporites* and *Illinites* (Potonié & Schweitzer, 1960; Grebe & Schweitzer, 1962; Clement-Westerhof, 1974). Within *L. virkkiae* there is a striking variability in shape and size of the sacci, including 'subsaccate' specimens with strongly reduced sacci, which are usually classified as *L. parvus* Klaus, 1963 (Clement-Westerhof, 1974). Despite the probability that many other saccate forms would require a broader morphological interpretation, the palynological diversity of the Bletterbach section still remains relatively high. The palynological record suggests that the local plant communities were relatively stable during the time of deposition of the Gröden/Val Gardena Sandstone (Pittau in Massari et al., 1994). This stability may reflect stable environmental conditions. Quantitative compositional differences between assemblages largely are related to taphonomic variables. A good example is the increased frequency (up to 25%) of *Nuskoisporites dulhuntyi* in some assemblages originating from fluvial deposits below the Cephalopod Bank. These very large monosaccate prepollen grains of *Ortiseia* (mean diameter 200 µm) are unsuitable for long-distance dispersal. Together with other remains of their parent plants, they exhibit a tendency toward burial close to the growing sites. By contrast, few grains will reach coastal/lagoonal depositional environments in the upper part of the Bletterbach section.

8. DISCUSSION

Prior to the discovery of the megafossil horizon in the Bletterbach Gorge it was widely believed that well-preserved plant fossils rarely occur in the Gröden/Val Gardena Sandstone and that the Bletterbach flora consisted principally of conifers and a few seed ferns (Clement-Westerhof, 1984, 1986, 1987; Poort & Kerp, 1990; Visscher et al. 2001). However, time-equivalent palynofloras (e.g., Klaus, 1963; Massari et al., 1994; Pittau et al., 2005) indicated that regional plant communities were much more diverse than suggested by the assemblages from the cuticle-bearing stratigraphic horizons. The discovery of plant megafossils with well-preserved cuticles (see Kustatscher et al., 2012, 2014, 2017), therefore, greatly contributed to a more accurate understanding of Euramerican late Permian plant communities.

The Bletterbach flora demonstrates that late Permian gymnosperm-dominated plant communities in the region that today is Southern Europe consisted of sphenopterids, peltasperms, putative cycadophytes, ginkgophytes and conifers. The high proportional abundance (i.e. >50% of specimens) of ginkgophyte fossils in the megafossil horizon is very unusual for Lopingian floras. Conifers represent approximately 40% of fossils in the megafossil horizon, while sphenophytes, seed ferns and putative cycadophytes (i.e. taeniopterid foliage) together comprise <5%. In contrast, the assemblage of the cuticle horizons clearly is dominated by conifer remains. The presence of lycophytes reported by Perwanger (1946) and Leonardi (1948, 1951, 1968) was not confirmed; fossils previously identified as lycophyte stems most likely represent defoliated conifer shoots or leaves of *Dicranophyllum*-like seed plants (Kustatscher et al., 2012).

The horizons containing the best-preserved fossils occur below and above the Cephalopod Bank, but plant remains also are found in several other horizons scattered throughout the section, from the so-called Knappenlöcher, at the bottom of the Bletterbach sequence, to the uppermost strata of the Gröden/Val Gardena Sandstone. Redbeds with gypsum layers and paleosols yield only a few compressed and partially permineralized stem sections composed mostly of pyrite, and rare casts of roots (Kustatscher et al., 2012). The abundance of plant remains in the layers around the Cephalopod Bank suggests that the higher conduciveness for plant preservation, and consequently a lesser taphonomic bias, was caused by marine transgression onto a distal fluvial-plain environment with meandering and abandoned channels. In this type of environmental setting, plants may become preserved in recognizable form even under generally semi-arid to arid conditions (Kustatscher et al., 2017). The size and quality of plant fossils from the megafossil horizon suggests a para-autochthonous assemblage. Support for this interpretation include the large, deeply dissected ginkgophyte leaves that often are intact and sometimes even occur in masses covering the bedding planes, as well as conifer shoots up to 30 cm long.

Permian plant fossil localities generally are rare in the Alps. Moreover, the few assemblages that have been recorded, e.g., Mölten/Meltina (Aspmair, 1998; Aspmair & Krainer, 1998), Neumarkt/Egna (Leonardi, 1948), Cuecenes (e.g., Florin, 1964; Leonardi, 1968), and several localities in the Vicentinian Alps (e.g., Clement-Westerhof, 1984) are mostly composed of only a few poorly preserved fragments of conifer shoots and petrified wood. Only *Germaropteris martinsii* occurs also in the Vicentinian Alps. The Val Trompia flora from the early Permian (Artinskian–Kungurian) Collio Formation is dominated by conifers (Remy & Remy, 1978; Visscher et al., 2001) and shares the occurrence of *Sphenopteris suessii* with the Bletterbach flora. The Kungurian Tregiovo plant assemblage from the upper Val di Non also is dominated by conifers (Forte et al., 2017), including narrow-leaved forms such as *Hermitia* Kerp et Clement-Westerhof, broad-leaved taxa including *Feysia* and *Quadrocladus*, and ovuliferous dwarf shoots assignable to *Dolomitia* and *Pseudovoltzia*. Moreover, ginkgophytes (*Sphenobaiera*), sphenopterids, callipterid peltasperms fronds (*Lodevia*) and ovuliferous structures (*Peltaspermum*), taeniopterids and sphenophytes (*Annularia* Sternberg, 1821; Marchetti et al., 2015) have been reported. Several of these taxa, such as *Sphenopteris*, *Peltaspermum* (=*Germaropteris*), *Taeniopteris*, *Sphenobaiera*, *Quadrocladus*, *Dolomitia* and *Pseudovoltzia* also are present in the Bletterbach flora.

The Bletterbach macroflora is correlative in geological age to the Zechstein flora from the Central European Basin, one of the most important Lopingian floras of Europe (e.g., Stoneley, 1958; Schweitzer, 1986; Uhl & Kerp, 2002). Other European plant assemblages of Lopingian age have been reported from Belgium (Florin, 1954), Poland (Czarnocki & Samsonowicz, 1913; Pajchlowa & Wagner, 2001), Hungary (Heer, 1876) and

Spain (Bercovici et al., 2009). All of these floras represent conifer-dominated plant assemblages. However, the presence of *Ullmannia*, the dominant taxon in all central European Zechstein assemblages, currently has not been documented in late Permian floras from southern Europe. Conversely, *Ortiseia*, *Majonica* and *Dolomitia*, which frequently occur in the Southern Alps, are exceedingly rare in Zechstein floras, with a few exceptions reported from the German Zechstein (e.g., *Ortiseia* and *Majonica*; Bödige, 2007). However, forms described as *Culmitzschia* Ullrich, 1964 from the German Zechstein may be identical to *Ortiseia*. The seed ferns *Germaropteris* and *Sphenopteris* occur in Zechstein and Bletterbach floras (Kustatscher et al., 2012, 2014), whereas alethopteroid pinnules have not been described from any other European Lopingian locality. Sphenopterids and putative cycadophytes have been recorded for several European fossil localities, although they are represented by different species. *Lesleya* is restricted to Germany and England, *Plagiozamites* and *Pseudoctenis* to England, whereas a single taeniopterid leaf fragment also has been found in Spain. Ginkgophytes typically are rare elements in Lopingian floras, with *Baiera* being the most common ginkgophyte in the German Zechstein and the Bletterbach floras (e.g., Weigelt, 1928; Stoneley, 1958; Schweitzer, 1962; Bauer et al., 2013, 2014). An additional, possibly ginkgophyte taxon from the German Zechstein is *Esterella* Boersma et Visscher, 1969, while the Bletterbach flora contains *Sphenobaiera* and several putative ginkgophyte leaves (Tab. 1). Another interesting aspect of the Bletterbach flora is the frequent occurrence of well-preserved cuticles. These remains are important not only as tools in the reconstruction of whole-plant taxa (Clement-Westerhof, 1984, 1986, 1987; Poort & Kerp, 1990), but also as proxy indicators in assessments of paleoenvironmental and palaeoclimatological conditions (Uhl & Kerp, 2005; Vörding & Kerp, 2008; Kustatscher et al., 2017). It should also be noted that the bulk-floral level of herbivory on the Bletterbach flora is comparable to that recorded for other Permian floras although generally low, also perhaps related to taphonomic biases (Wappler et al., 2015; Labandeira et al., 2016).

Moreover, palynological assemblages indicate that the regional late Permian flora must have been even more diverse than suggested based on the macrofloral remains. Preceeding the Permian–Triassic biosphere crisis, there is recognition of some palynological signs of terrestrial ecosystem destabilization in the Bellerophon Formation. Together with many other Permian saccate pollen types, the characteristic coniferous elements (*Nuskoisporites dulhuntyi*, *Lueckisporites virkkiae*, *Jugasporites delasaucei*) exhibit their last occurrences, while lycopsid microspores become more common in the Early Triassic when *Densoisporites*, *Lundbladispora* and *Kraeuselisporites*) enter the record. The proportion of *Reduviasporonites* shows an increase toward the top of the Bellerophon Formation (Visscher et al., 1996). In the Bletterbach section, the succeeding Tesero Member of the Werfen Formation is palynologically barren, but elsewhere in the Dolomites Region the basal part of this unit is characterized by a marked proliferation of *Reduviasporonites*. Considering the plausibility that *Reduviasporonites* represents soil-born fungi, elevated amounts of it have been interpreted as evidence for increased soil erosion at the end of the Permian (Visscher et al., 2011). This concept is consistent with the presence of soil-derived plant debris in latest Permian sediments of the Dolomites (Sephton et al., 2005a). At the molecular level, elevated levels of aromatic hydrocarbons confirm an intensified burial flux of soil-derived precursor materials (Sephton et al., 1999, 2005b).

9. CONCLUDING REMARKS

During the Permian, Euramerica was characterized by a progressive trend towards drier climates (e.g., Kerp, 1996, 2000; Roscher & Schneider, 2006; Montañez et al., 2007). This aridification, although interrupted during several periods of more humid conditions (Roscher & Schneider, 2006; DiMichele et al., 2008), had a profound impact on the overall composition of the terrestrial flora and fauna (DiMichele et al., 2008). The main fossiliferous horizon (megafossil horizon) of the Bletterbach were deposited in a deltaic system subjected by a marine transgression from the east and continued sediment influx from the west. The dark and heterolithic shales, which are rich in plant fragments, originated from interdistributary bays and delta-plain wetlands. Above the Cephalopod Bank, for instance the cuticle horizon, the regression resulted in progradation of a channel-floodplain system closely resembling the lithofacies exposed below the Cephalopod Bank (Kustatscher et al., 2017; Bernardi et al., 2017). Moreover, sea-level changes may have influenced vegetational composition during this period of time. A sea-level highstand during the middle Wuchiapingian resulted in the principal Zechstein transgression (Legler et al., 2011; Legler & Schneider, 2013), which likely corresponded to the Cephalopod Bank in the Bletterbach succession (Kustatscher et al., 2014). The marine transgression would move first the azonal, coastal flora into the taphonomic window of the Bletterbach Gorge and then establish a distal fluvial plain with meandering and abandoned channels, which ideally would be the best environment for establishment of a rich and varied flora, typical of an intrazonal flora, along river channels, oxbow lakes and local ponds. Such a flora would result in the presence of a lusher and richer vegetation (Kustatscher et al., 2017). Due to the high sedimentation rates, the preservation potential was considerably higher than in other sedimentary settings. This resulted in a locally higher diversity and atypical quantitative compositions of various fossil assemblages in the megafossil horizon. By contrast, even the composition of the megafossil horizon did not reach the regional diversity displayed in palynological samples. Moreover, the extent to which insect herbivores accessed this flora was modest, confined only to 16 damage types (DTs). Although the majority of Bletterbach interactions were generalized when assessed by abundance, there were considerably more specialized interactions when evaluated by DT diversity. It is anticipated that ongoing and future research will continue to provide additional data and on the composition and paleoecology of the unique Bletterbach flora.

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