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GINKGOPHYTES FROM THE UPPER PERMIAN OF THE BLETTERBACH GORGE (NORTHERN ITALY)

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Abstract. Fossil evidence of late Palaeozoic ginkgophytes is rare; Palaeozoic floras in which ginkgophytes are abundant or represent a predominant element have not previously been described. The late Permian (Lopingian) flora from the Gröden/Val Gardena Sandstone of the Bletterbach gorge in the Dolomites (northern Italy) contains an unusually large proportion of ginkgophytes. The fossils include the foliage taxa *Baiera digitata* and *Sphenobaiera* sp., as well as putative *O-ha-tsuki*-type fertile leaves, seeds, and several ginkgophyte-like leaf types of uncertain affinities. Local mass occurrences of ginkgophyte leaves have also been observed. The Bletterbach flora suggests that ginkgophytes were important elements in certain vegetation types (probably forests) as early as the late Permian.

Introduction

The ginkgophytes are an ancient lineage of gymnosperms believed to have originated during the late Palaeozoic (Taylor et al. 2009; Zhou 2009). However, the fossil record of these plants from the Palaeozoic remains sparse; Palaeozoic floras characterized by an abundance or even predominance of ginkgophytes have not been described to date. Therefore, our understanding of the origin, early evolutionary history, and palaeoecology of this group remains incomplete.

The flora from the Gröden/Val Garden Sandstone of the Bletterbach gorge in the Dolomites (Lopingian, northern Italy) is noteworthy among the late Permian floras worldwide because some of the fossiliferous layers contain a relatively high proportion (>50%) of ginkgophyte fossils. However, the ginkophyte record from Bletterbach has not been comprehensively documented to date.

This paper provides a systematic overview of the ginkgophyte fossils from Bletterbach with descriptions of the most abundant types, and evaluates the significance of the ginkgophyte richness and diversity at this locality. The Bletterbach assemblage suggests that ginkgophytes were important elements in certain vegetation types (probably forests in fluvial/deltaic plains) as early as the late Permian, much earlier than previously thought. Fossil assemblages rich in ginkgophytes have previously been documented only from Mesozoic sediments (Late Triassic-Early Cretaceous; e.g., Harris, 1935; Krassilov 1972; Harris et al. 1974; Li et al. 1988; Zhou 2009).

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Geological setting, material and methods

Stratigraphy and age

The Bletterbach gorge is located between the villages Aldein/Aldino and Radein/Redagno in the western part of the Dolomites (northern Italy; Fig. 1). Since 2009 the site is part of the Unesco World Heritage "Dolomites". The gorge exposes a complete stratigraphic succession ranging from the early Permian Athesian Volcanic Group at base to the early Middle Triassic Contrin Formation at top of the Weisshorn/Corno Bianco (e.g., Avanzini et al. 2007; Marocchi et al. 2008; Kustatscher et al. 2012).

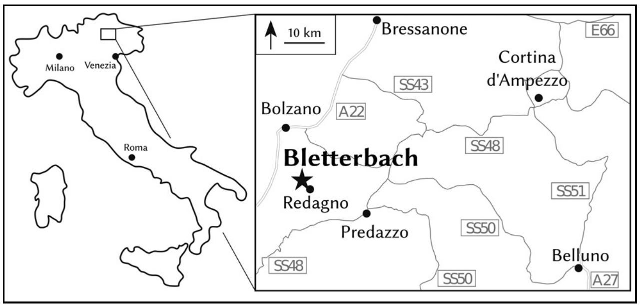

Fig. 1 - Geographical map with the Bletterbach locality indicated (black asterisk)

Plant fossils occur in several horizons within the late Permian Gröden Sandstone/Arenaria della Val Gardena. The Gröden Sandstone is characterized by alternating layers of red to greyish fluvial siliciclastics and evaporites or carbonate-siliciclastics, suggesting different depositional environments. Gypsum horizons, interpreted as continental sabkhas, occur within the reddish mudstones (Massari et al. 1988). Calcic soils with local vertical features are interpreted as palaeosols (Wopfner & Farrokh 1988). They display a semi-arid to dry-subhumid climate characterized by strong seasonality (Cassinis et al. 1999). Approximately 80 m above the base of the Gröden Sandstone marine influence becomes evident through a change from the reddish to grey and blackish colours, and increased carbonate content. A marine horizon, about 2 m thick (Cassinis et al. 1999) and containing a sparse cephalopod fauna (Broglio Loriga et al. 1988), characterizes the maximum flooding surface. Its erosion-resistant limestone forms the top of the waterfall in the Butterloch. For more details, see Kustatscher et al. (2012). The mudstone horizons above this marine bed represent a marine regression and contain plant fossils with well-preserved conifer and seed fern cuticles (the so-called "cuticle horizon"; e.g., Clement-Westerhof 1984, 1986, 1987); this horizon also contains rare ginkgophyte remains. After tens of metres of continental sediments comparable to the lower part of the formation, the transition of the Gröden Sandstone to the Bellerophon Formation follows, which is characterized by an interfingering of fluvial and coastal or lagoonal deposits. The section is capped by a transgressive sequence. The Gröden Sandstone has been dated as Wuchiapingian (early Lopingian) based on palynomorphs and footprints (Pittau 2005; Avanzini et al. 2011).

Material and methods

The majority of fossils used in this study comes from one horizon (informally called the "new horizon") located approximately 1-2 m below the waterfall (see above). The specimens are preserved as black compressions or, in rare instances, greyish impressions on a greyish to reddish sandstone matrix. Most of the fossils (specimen numbers preceded by "NMS PAL") were collected by authors RB and TCF. All specimens are kept in the Museum of Nature South Tyrol in Bozen/Bolzano (Italy).

An additional suite of fossils included in this study was collected in the 1970s from the "cuticle horizon" located above the waterfall. These specimens, which occur as black compressions on a dark grey mudstone matrix, are housed in the Laboratory of Palaeobotany and Palynology, University of Utrecht, the Netherlands (specimen numbers preceded by "UU").

All fossils were photographed with a Canon Eos D550 digital camera and the images processed in Gimp 2.8.

Results and Discussion

The Bletterbach fossil collection used in this study consists of 478 rock slabs containing 1897 identifiable vegetative and reproductive plant parts. The assemblage is characterized by a high proportional of ginkgophyte remains (i.e. >50% of total plant fossils in the "new horizon") that sometimes occur in masses on the bedding plane (see Fig. 3D). Approximately 39% of the specimens from the "new horizon" are conifers. Sphenophytes, ferns, pteridosperms, and putative cycadophytes (i.e. taeniopterid foliage) together comprise less than 5% of the specimens. Most ginkgophyte fossils represent foliage remains assignable to the genera *Baiera* and *Sphenobaiera*. Approximately 6% of the specimens represent fragments of narrow linear leaves that probably also belong to the ginkgophytes.

The "cuticle horizon" contains significantly fewer ginkgophyte remains; the assemblage is dominated by conifers (e.g., Clement-Westerhof 1984, 1987).

Baiera digitata (Brongniart) Heer, 1876

The collection contains 15 well preserved specimens confidently assignable to *Baiera digitata*; however, only four of them are more or less complete leaves (e.g., Fig. 2A, B, D, E). More than 100 specimens represent leaf fragments (35-117 mm long and 18-67 mm wide) displaying the characteristic subdivision into petiole and lamina, and thus can also be assigned to *B. digitata* with some confidence. The lamina is wedge-shaped, usually longer than wide, and subdivided into at least two symmetrical primary segments, each up to 10 mm wide. The two segments fork a second time, sometimes also a third time. Primary and all secondary segments fork at about the same distance from the lamina base, resulting in a regular branching pattern. Individual leaf segments are linear to slightly elliptical or spindle-shaped, entire-margined, and, where preserved, show a somewhat convex apex. Up to 8 parallel veins occur in the ultimate segments (Fig. 2C). The basal angle between the outer segments varies from 37° to 72°.

Discussion. Foliage of this type was informally denoted "Ginkgophyte type 2 resembling *Sphenobaiera digitata* (Brongniart) Florin, 1936" in a preliminary account on the Bletterbach flora (Kustatscher et al. 2012). However, Bauer et al. (2013a) recently reinforced that ginkgophyte leaves subdivided into petiole and lamina must not be assigned to *Sphenobaiera*, because the original diagnosis characterizes *Sphenobaiera* as lacking a distinct petiole (see Florin 1936a, b). The leaves described here all possess a distinct petiole (e.g., Fig. 1A) and thus are assigned to *Baiera digitata*. Florin (1936a, b) included not only the petiole in his generic diagnosis, but also regarded the presence of only 2-4 veins per ultimate leaf segment as a diagnostic feature of *Baiera*. However, the Bletterbach leaves possess up to 8 veins per leaf segment, thus arguing against assigning these fossils to *Baiera*. Harris et al. (1974) suggested that fossil ginkgophyte leaves with more than 4 veins per segment should be assigned to *Ginkgo* L. (or *Ginkgoites* Seward). However, vein numbers >4 have also been noted in other *Baiera* species, including *B. tartarica* Zalessky, 1929 from the Permian of Russia and *B. raymondii* Renault, 1888 from the Permian of France. In addition, assignment of the Bletterbach fossils to *Ginkgo digitata* would create considerable taxonomic and nomenclatural confusion and is, therefore, not advisable. A complete revision of all *Baiera* fossils is necessary to determine the diagnostic value of vein number per segment in all these leaves.

Sphenobaiera sp. A

Eight nearly complete leaves from Bletterbach are assignable to *Sphenobaiera* sp. A (Fig. 3B). Specimens are 60-89 mm long and 20-40 mm wide; a petiole is lacking. Some specimens show a distinct thickening around the base that might represent abscission tissue (Fig. 3E, arrow). The leaves fork once close to the base (Fig. 3B), with each of the two segments up to 12 mm wide and occasionally deeply incised. Segments are broadly lanceolate in shape (with the greatest width in the middle part) and the apex is convex or pointed. Several delicate veins extend parallel in longitudinal direction and bifurcate several times. However, the exact number of veins per leaf segment cannot be determined because the coaly substance of the leaves is thicker than in *B. digitata* fossils. The angle between the basal segments varies between 30° and 50°.

Discussion. In their preliminary account on the Bletterbach flora, Kustatscher et al. (2012) tentatively denote this foliage type as "Ginkgophyte type 1 with a general affinity to the leaf genus *Sphenobaiera*".

The fossils are assigned to *Sphenobaiera* because they do not show a petiole. *Sphenobaiera* sp. A from Bletterbach differs from *S. digitata* from the lower Permian of Thuringia (Germany: Arnhardt 1968; Barthel 2007) in the number and shape of leaf segments, i.e. the latter is characterized by 4-5 primary segments, while *Sphenobaiera* sp. A is characterized by only two primary segments, which, however, may be deeply incised, hence giving the impression of 4 secondary segments. Moreover, the leaf segments in *S. digitata* from Germany are linear and narrow (strap-shaped, <2 mm wide), while the segments of *Sphenobaiera* sp. A are broadly lanceolate and up to 12 mm wide. *Sphenobaiera* sp. A differs from *Sphenobaiera micronervis* Wang et Wang, 1986 from the upper Permian of China by the width of the leaf segments, which is 0.5-0.7 mm in *S. micronervis*, and up to 12 mm in *Sphenobaiera* sp. A. *Sphenobaiera* leaves have also been reported from the Permian of Antarctica (Taylor & Taylor 1993); however, these fossils actually are Carnian (Late Triassic) in age (pers. comm. Benjamin Bomfleur and Rudolph Serbet, 2013).

Fertile foliage and seeds

More than 25 compressed ovules/seeds with likely affinities to the ginkgophytes also occur in the Bletterbach collection. Ovules/seeds are roundish to ovoid, up to 1.3 cm long and 1 cm wide; a basal collar-like structure, which is characteristic of modern *Ginkgo* seeds (see Fuji 1896), is lacking (Fischer et al. 2010).

Two of the ovules/seeds appear to be attached to *Baiera digitata*-type leaves (e.g., Fig. 3C). Fischer et al. (2010) compare this type of ovule/seed attachment to leaves to a phenotypical aberration of sporadic occurrence in modern *Ginkgo biloba* from Japan that is known as *O-ha-tsuki* (Fuji 1896). However, the fossils that form the basis for Fischer et al. (2010) are far from excellently preserved, and thus render it difficult to determine as to whether ovule/seed attachment is real or represents a taphonomical artefact. Nevertheless, the close association of the ovules/seeds with *B. digitata* type foliage may suggest that both were produced by the same plant. Adding support for this hypothesis is the fact that the epidermal anatomy of the ovules/seeds is very similar, if not identical, to that of the associated *B. digitata* leaves (Fischer et al. 2010).

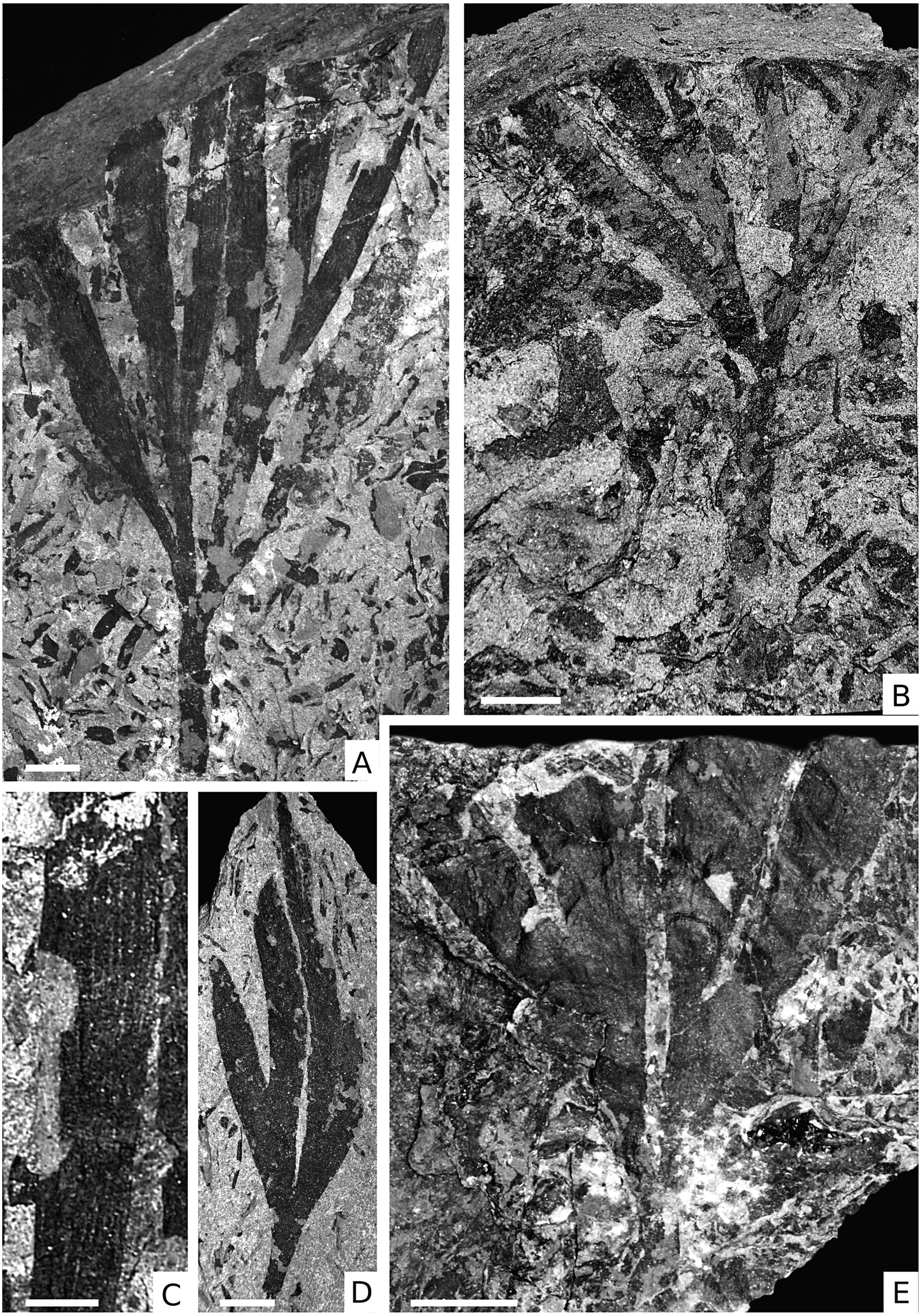

Fig. 2 - *Baiera digitata* (Brongniart) Heer, 1876; Scale bar = 1 cm if not otherwise indicated.
A) Four times-bifurcate specimen showing a distinct petiole (NMS PAL2061); B) Three times-bifurcate leaf with petiole (NMS PAL 1436); C) Detail of Fig. 1A showing venation of lamina segment; scale bar = 0.5 cm; D) Twice-bifurcate leaf (NMS PAL1445); E) Twice-bifurcate leaf with relatively wide segments and clear venation (NMS PAL2188).

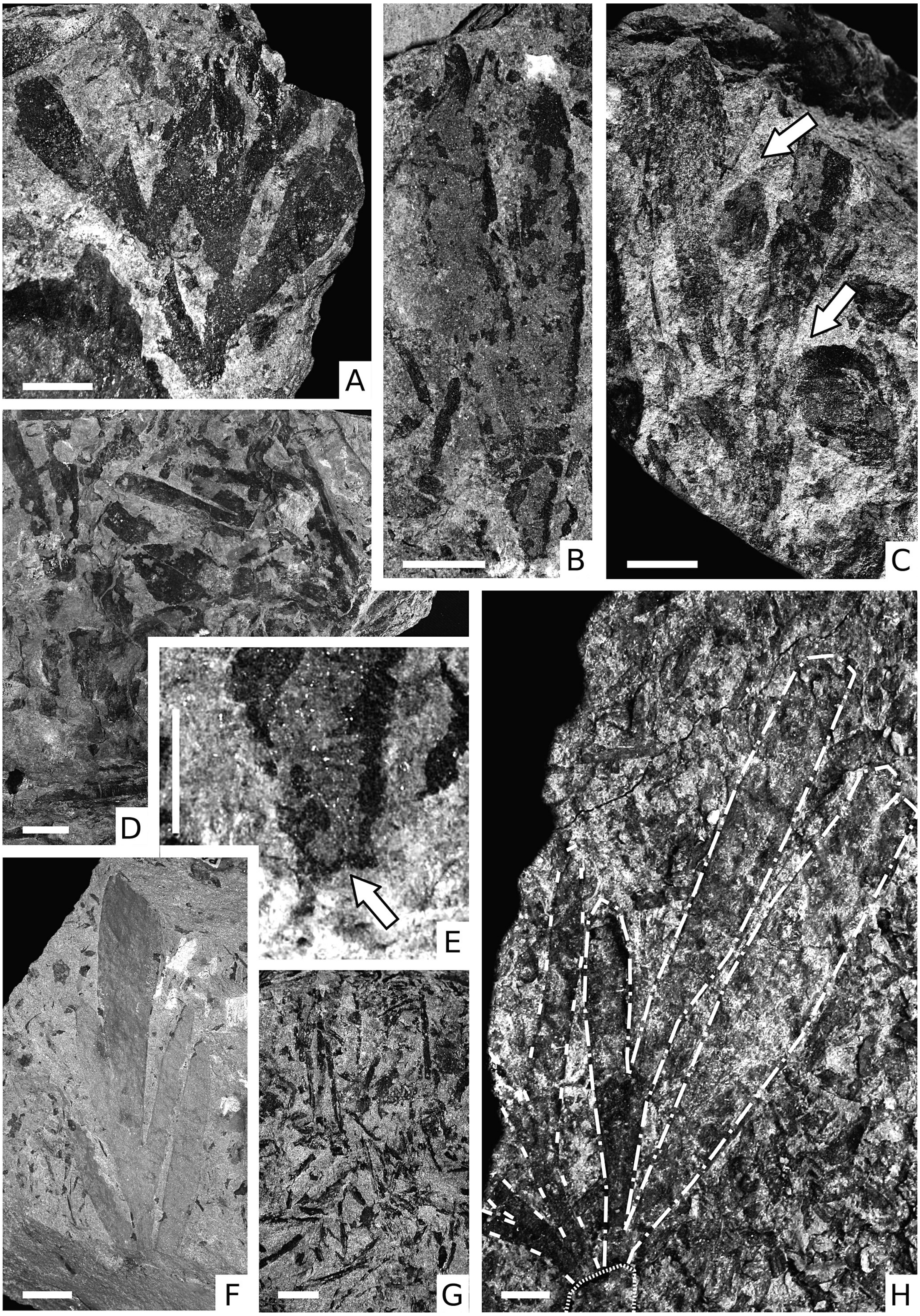

Fig. 3 - Scale bar = 1 cm if not otherwise indicated.
A) Enigmatic leaf type 3; several times forked leaf or branched axis with club-shaped leaves (NMS PAL928); B) *Sphenobaiera* sp. A, once-bifurcate leaf with complete leaf base (NMS PAL861); C) *O-ha-tsuki*-type leaf with what appear to be two seeds (arrows) attached to lamina (NMS PAL2186; from Fischer et al., 2010, Fig. 3); D) Mass occurrence of ginkgophyte leaves (NMS PAL2197); E) Detail of Fig. 3B showing the abscission area (arrows); F) Enigmatic leaf type 2 (NMS PAL1468); G) Enigmatic leaf type 1 (NMS PAL 2014); H) Shoot segment (freckled line) with two attached leaves (chain line right leaf; left dashed line) (UU 24097).

Shoot segment with attached ginkgophyte leaves

The Utrecht collection holds one specimen from the "cuticle horizon" (Fig. 3H) of a shoot segment with two leaves in physical connection. The specimen shows what we believe are two *Sphenobaiera*-type leaves attached to the tip of a shoot (Fig. 3H). While the leaf on the left side is fragmentarily preserved, but still shows two orders of bifurcations, the leaf on the right side is more complete. It shows three orders of bifurcations, the first dividing the leaf into two primary segments while the second and third are only present in the left primary segment. Moreover, the ultimate segments show a probable distal indentation (Fig. 3H).

Enigmatic foliage fossils

In addition to the bona fide ginkgophyte remains, there are three foliage fossil types from Bletterbach that probably represent ginkgophytes, but that cannot be assigned to this group of plants with confidence for various reasons.

1) This leaf type is represented by fragments up to 5 mm wide and variable in length. In some instances, forking into 2-3 segments occurs in these fragments (Fig. 3G), with each of segment having a single vein. The fragments resemble leaves of *Trichopitys*, *Polyspermophyllum* and *Dicranophyllum*. On the other hand, the presence of only one vein could also indicate affinities to the Czekanowskiales or conifers.

2) The second enigmatic leaf type is represented by a single impression (part and counterpart) of a large leaf (Fig. 3F), which is more or less wedge-shaped and characterized by an elongate and distally enlarged middle segment. The lamina is 102 mm long and 45 mm wide. Unfortunately, the proximal portion of the leaf is not preserved, and thus it remains uncertain whether it was petiolate. The lamina consists of five segments. From the proximal part of the middle segment three relatively small lateral segments arise, which are more or less lanceolate, 7-9 mm wide and 5-6 cm long, and appear to taper towards the tip. Distally, the middle segment is subdivided (or deeply incised) into two segments, one of which distinctly larger than the other. The larger of the two middle segments is inversely lanceolate and increases in width (up to 19 mm) towards the tip, which is not preserved. The basal angle between the outer segments is about 45°. Numerous tenuous, bifurcating veins are present; however, determining the exact number of veins is impossible due to preservation.

Discussion. This leaf resembles the attached leaves illustrated in Fig. 3H in size and basic morphology. It differs from other late Palaeozoic bona fide ginkgophyte foliage in its irregular subdivision of the lamina, but somewhat resembles certain members of the enigmatic genus *Psygmophyllum*. However, the Bletterbach fossil differs from all Permian *Psygmophyllum* species because of the shape of the individual leaf segments. The lateral segments of the Bletterbach fossil are lanceolate, while the middle segment is inversely lanceolate with an increasing width toward the apex. Conversely, these segments are cuneate in *Psygmophyllum flabellatum* (Lindley et Hutton) Schimper, 1870 from the Permian of Great Britain, obovate to wedge-shaped in *Psygmophyllum expansum* (Brongniart) Schimper, 1870 from the Permian of Russia, elongated cuneate in *Psygmophyllum cuneifolium* Brongniart, 1870 from the Permian of Orenburg (Russia), and elongate linear but broadened slightly in the middle in *Psygmophyllum ctenoides* (Goeppert) Schimper, 1870 from the Permian of Silesia (Germany). The Bletterbach leaf differs from *Psygmophyllum intermedium* Naugolnykh, 2012 from the lower Permian of the Urals with regard to general shape. *Psygmophyllum intermedium* leaves are composed of a stipe and two asymmetrical blade portions.

3) Only one specimen belongs to the third leaf type. Specimen NMS PAL 928 (Fig. 3A) is 83 mm long and 81 mm wide with a basal angle of about 80°. It corresponds to a multibranched system, the ultimate segments of which are club-shaped with a maximum width of up to 14 mm.

Discussion. The system either represents a leaf forking several times or, more likely, a branched axis of some sort bearing club-shaped ultimate segments, perhaps leaves. We have decided to illustrate and briefly describe this fossil here solely because it is the largest putative ginkgophyte fossil discovered from the Bletterbach locality to date.

General discussion

The flora from the Bletterbach gorge is notable among the European Late Permian floras for its high proportional of ginkgophyte fossils, i.e. more than 50% of total plant fossils of the "new horizon". Approximately 39% of the specimens from this horizon are conifers, while other gymnosperms (e.g., seed ferns and putative cycadophytes) and vascular cryptogams (e.g., sphenophytes) are rare (together <5% of the specimens; see Kustatscher et al. 2014). Most ginkgophyte fossils are impressions/compressions of foliage assignable to *Baiera digitata* and *Sphenobaiera* sp. A. Approximately 6% of the flora are fragments of narrow strap-shaped leaves that resemble foliage produced by the Dicranophyllales or Czekanowskiales, and club-shaped or several times-bifurcate leaves with possible affinities to the ginkgophytes or some other group of seed plant. Especially interesting are several mass occurrences of (highly fragmented) ginkgophyte leaves (Fig. 3D).

Plant fossils from Bletterbach, including the (putative) ginkgophytes, are generally highly fragmented and do not normally show many details of the macromorphology; larger specimens showing different parts of a plant in physical connection are exceedingly rare. This may suggest that the plant remains have been exposed to mechanical forces, transport, and decomposition in water for an extended time prior to embedding. The Gröden Sandstone represents a fluvial system (Massari et al. 1988) or part of a much larger flood plain with the main distributary channels located outside the gorge (pers. comm. Matthias Franz, 2013). It is, therefore, also possible to envision that the source plants grew upstream and were transported some distance into their depositional environment through the distributary channel; if this is accurate, then the mass occurrences could be a result of local accumulation of leaves through water currents in river bends or banks.

Natural populations of extant *Ginkgo biloba* apparently no longer exist; even the famous occurrences in China that have been suggested as representing natural populations are now known to have been affected by humans (e.g., Niu et al. 2011). Consequently, the growth of fossil ginkgophytes (e.g., as solitary trees or in stands or dense forests) cannot be directly inferred from comparison with modern relatives. Mass occurrences of ginkgophyte leaves and leaf fragments have repeatedly been observed in the Bletterbach locality, and might reflect seasonality. The extant *G. biloba* sheds its foliage once per year, in autumn, and does not produce new leaves until the following spring. Cassinis et al. (1999) interpreted the sedimentary sequence of the Gröden Sandstone as reflecting strong seasonality. The ginkgophytes are generally regarded as representing a conservative group of plants, and late Permian representatives perhaps shed their leaves once per year, precisely as *G. biloba*. An alternative speculation could be that a storm event caused unnatural shedding of large numbers of leaves which subsequently became accumulated in the depositional environment.

Since the Bletterbach flora is the only late Permian flora known to be characterized by a high proportional of ginkgophyte fossils, it cannot be directly compared with any other late Permian flora in this regard. The only other Permian flora displaying a considerable diversity in ginkgophytes is the German Kupferschiefer flora, albeit the latter is probably somewhat older geologically (Bauer et al. 2013a). The dominant plants in the Kupferschiefer flora are conifers; *Baiera digitata* is the most common ginkgophyte (Haubold & Schaumberg 1985). On the other hand, *Sphenobaiera* has not been reported from the Kupferschiefer flora, while this taxon is relatively common in the Bletterbach gorge.

Ginkgophytes are not only abundant in the Bletterbach flora, but there appears also to be some diversity. As a result, the fossils described in this paper are important with regard to a more accurate understanding of the late Palaeozoic fossil record of the ginkgophytes. Many ginkgophyte fossils from Bletterbach are difficult to interpret due to their meagre preservation quality, incompleteness, and/or lack of diagnostic features. Nevertheless, we believe that it is necessary to record these fossils as a first step in our ability to ultimately understand the evolutionary history of the ginkgophytes. We anticipate that, as more information is gathered about late Palaeozoic ginkgophytes, some of the questions with regard to the evolutionary history and palaeobiology of this interesting and ancient lineage of seed plants will be more fully understood.

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