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Middle Miocene macrofloral elements from the Lavanttal Basin, Austria, Part I. *Ginkgo adiantoides* (Unger) Heer

Barbara MELLER[1], Reinhard ZETTER[1], Andreas HASSLER[2], Johannes M. BOUCHAL[1], Christa-Charlotte HOFMANN[1] & Friðgeir GRÍMSSON[1]*

[1] University of Vienna, Department of Paleontology, Althanstraße 14 (UZA II), A-1090 Vienna, Austria;

[2] Burgstall-St.Andrä 99, 9433 St. Andrä, Austria;

*) Corresponding author, fridgeir.grimsson@univie.ac.at

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Abstract

A new locality, at Schaßbach (Carinthia, Austria), within the Neogene Lavanttal Basin has yielded numerous well preserved early Badenian (Langhian) plant macrofossils. This paper, which is the first in a series of papers that describe the macrofossil remains from Schaßbach, provides a geological and chronostratigraphic framework of the study area and summarizes previous research on plant macrofossils from the Lavanttal Basin. Here, Cenozoic leaf fossils of *Ginkgo* with preserved cuticles showing epidermal features are described for the first time from Austria, and from the pre-Pliocene of the Central Paratethys region. The *Ginkgo* foliage remains are currently one of the oldest Cenozoic fossils representing this genus in Central Europe. The fossils are considered to reflect trees growing outside lowland wetland areas and originated from the riparian vegetation. Based on the current habitat and fossil occurrence of Cenozoic ginkgos, the early Badenian flora in the Lavanttal area likely endured a warm temperate and humid climate.

Aus der neuen Lokalität Schaßbach (unteres Badenium, unteres Langhium) im neogenen Lavanttal Becken wurden zahlreiche gut erhaltene Pflanzenfossilien gesammelt, die derzeit untersucht werden. In der vorliegenden Arbeit wird ein geologischer Überblick gegeben, frühere paläobotanische Arbeiten werden zusammenfassend dargestellt und das erste systematisch untersuchte Makroflorenelement aus Schaßbach wird beschrieben: Ginkgoaceae. Känozoische Blattfossilien von *Ginkgo adiantoides* (Unger) Heer mit gut erhaltenen Kutikularstrukturen sind hier zum ersten Mal aus Österreich und dem prä-Pliozän der Zentralen Paratethys Region beschrieben. Die *Ginkgo*-Blätter aus Schaßbach repräsentieren derzeit eines der ältesten Vorkommen der Gattung im Känozoikum Mitteleuropas. Die Bäume wuchsen vermutlich außerhalb der niedrig gelegenen Feuchtgebiete als Teil der orographisch höher gelegenen Umgebungsvegetation. Anhand der heutigen und fossilen Vorkommen lässt sich vermuten, dass die mittelmiozäne (Unter-Badenium) Flora des Lavanttals unter warm gemäßigtem und humidem Klima wuchs.

1. Introduction

A new middle Miocene (early Badenian; Langhian; ca. 16-14 Ma) fossil locality at Schaßbach, in Lavanttal, Carinthia, Austria, is extremely rich in plant macrofossils, particularly leaf imprints and leaf compressions. Recently, this locality has yielded numerous exceptionally well-preserved leaves, fruits, seeds, cones, and other plant remains, as well as fossil insects, fish skeletons, and vertebrate remains. The focus of this research group is on the plant macrofossils from the middle Miocene of the Lavanttal Basin, with special emphasis on the Schaßbach locality.

The Lavanttal Basin provides a semi-continuous record of freshwater and brackish sediments with terrestrial plant fossils from the Karpatian (late early Miocene) to early Pannonian (early late Miocene), spanning a time period from ~17 Ma to ~11 Ma (e.g. Beck-Mannagetta, 1952; Reischenbacher and Sachsenhofer, 2013). Preliminary investigations from several stratigraphic levels within the basin show that most successions contain plant macrofossils and well-preserved pollen and spores. This suggests that the Lavanttal Basin has the potential to provide unique information, based on terrestrial proxies, about the vegetation evolution and climatic history in this part of the Central Paratethys, during the Middle Miocene Climatic Optimum (MMCO, 17-14.5 Ma) and shortly thereafter. The MMCO is considered to be a period in which deep oceans were much warmer and temperatures at mid-to-high latitudes were considerably higher than at present (e.g., Zachos et al., 2001; Pound et al., 2012).

Continuous plant fossil records that span this critical time period and come from the same geographical area are rare, but potentially could illuminate important regional changes in the vegetation and local climate signals (e.g., Kovar-Eder et al., 1994; Kvaček et al., 2006; Denk et al., 2013); these are crucial to fully understand phytogeograhic patterns and the middle to late Miocene Northern Hemispheric climate evolution. Thus the long term aim is to provide a taxonomic account (based on gross morphology and cuticular/anatomical analyses) of the macrofloras spanning the Karpatian to Pannonian interval in the Lavanttal Basin and their contemporaneous palynofloras, based on combined light microscopy (LM) and scanning electron microscopy (SEM) investigations (e.g., Grímsson et al.; 2011, 2015; Grímsson and Zetter, 2011). The combined macro- and palynofloras can then be used to reconstruct the vegetation at various stages during the time span investigated, and document the floral changes and climate evolution in this region during and following the critical MMCO period. This will eventually provide an important link in the palaeoecological framework of the Lavanttal Basin and ist surroundings, and offer a realistic reconstruction of the environments sustaining the terrestrial (semiaquatic) vertebrate fauna, including turtles (Trionychidae), crocodiles, otters (Mustelidae), rhinoceros (Rhinocerotoidae), dormice (Gliridae), boars (Suidae), *Palaeomerix* (an extinct Ruminantia), songbirds (Passeriformes) and primates (*Dryopithecus*) thriving in this area at that time (e.g., Mottl, 1957; Wank, 1991; Happ, 2014).

2. Previous studies on macrofloras from the Lavanttal Basin

The middle to upper Miocene sediments of the Lavanttal Basin have yielded several plant macrofossils over the last 160 years (Table 1). Although most work on the Lavanttal macrofloras was conducted prior to ~1960, the published floras have never been revised. Lipold (1854) mentioned plant remains from Wiesenau and Schlott, just north of the Lavanttal Basin, determined later by Franz Unger and listed by Lipold (1856). Zwanziger (1872) also mentioned a few leaf fossils from St. Andrä, in the western central part of the Lavanttal Basin. The first comprehensive overview on fossiliferous localities and their plant macrofossil content from the Lavanttal Basin was presented by Zwanziger (1876), including the Dachberg, Wiesenau, St. Andrä, Wolfsberg, and St. Leonhard localities (see Table 1). The "Cypriniden-marls" of Siegelsdorf, a locality just north of the new Schaßbach locality, yielded several leaf fossils that were described but not figured by Zwanziger (1881, 1882). Later, Hofmann (1929) distinguished about 60 plant taxa from various localities within the Lavanttal Basin, but did not illustrate any specimens. Hofmann also described *Ficus*

Middle Miocene Lavanttal Basin

	Lower Badenian			
Locality	Mühldorf	Windisch Grutschen	Schönweg	Schaßbach
Latitude and longitude (ca.)	46°44'09"N, 14°51'34"E	46°44'09"N, 46°41'33"E	46°44'30"N, 14°56'26"E	46°47'52"N, 14°48'20"E
Previously identified macrofloral elements	*Glyptostrobus europaeus* (ls), *Pinus* sp. (c), Betulaceae (l), *Buxus* sp. (l), *Cinnamomophyllum scheuchzeri* (l), *Daphnogene* sp. (l), *Dicotylophyllum* spp. (l), *Engelhardia orsbergensis* (l), *Engelhardia macroptera* (d), *Lauraceae* (l), *Myrica lignitum* (l), *Platanus leucophylla* (l), *Platanus neptuni* (l), *Quercus* cf. *kubinyii* (l), *Quercus* spp. (l), cf. *Trigonobalanopsis* sp. (l), *Carya* sp. (d)	*Cinnamomophyllum scheuchzeri* (l)	*Cyperaceae* indet., *Acer* sp. (d), *Acer trilobatum* (l), *Alnus julianaeformis* (l), *Alnus kefersteinii* (l), *Araliophyllum denticulatum* (l), *Artocarpidium serratifolium* (l), *Banksia ungeri* (l), *Ceanothus tiliaefolius* (l), *Cinnamomum lanceolatum* (l), *Cinnamomum* sp. (l), *Cinnamomophyllum scheuchzeri* (l), *Cinnamomophyllum* cf. *polymorphum* (l), *Daphnogene lanceolata* (l), *Daphnogene spectabile* (l), *Daphnogene polymorpha* (l), *Daphnogene* sp., *Elaeodendron haeringianum* (l), *Engelhardia detecta* (l), ?Fagaceae indet. (l), *Fagus castaneifolia* (l), *Ficus* sp., *Ficus tenuinervis* (l), ?Juglandaceae indet. (l), *Laurus tetrantheroides* (l), *Litsea* sp. cf. *asiatica* (l), *Myrica acutiloba* (l), *Planera ungeri* (l), *Populus geinitzii* (l), *Prunus palaeocerasus* (l), *Quercus drymeja* (l), *Quercus goepperti* (l), *Quercus* sp. (l), *Sapindus falcifolius* (l), *Sapotacites sideroxyloides* (l)	
For geological background and plant fossils see	Berger 1955; Meller and Kvaček 2007	Berger 1955	Hofmann 1929; Berger 1955; Knobloch 1977	This study
	Middle Badenian			
Locality	Ölbach (=Elbach)	Plästetten	Ettendorf	Lavamünd
Latitude and longitude (ca.)	46°40'18"N, 14°56'59"E	46°39'16"N, 14°56'55"E	46°40'19N, 14°56'58"E	46°38'34"N, 14°56'26"E
Previously identified macrofloral elements	cf. *Castanea atavia* (l), ?*Quercus mediterranea* (l), ?*Quercus drymeja* (l), *Quercus neriifolia* (l), *Zelkova ungeri* (l), *Cinnamomophyllum scheuchzeri* (l)	*Cinnamomophyllum scheuchzeri* (l)	*Taxodioxylon sequoianum* (d)	*Dryandroides lignitum* (l), *Quercus drymeja* (l)
For geological background and plant fossils see	Berger 1955	Berger 1955	Hofmann 1929	Zwanziger 1881; Hofmann 1929

Table 1: Currently known Miocene plant macrofossil localities within the Lavanttal Basin. Note: Some of these floras are currently under study. The taxa mentioned in this table have their original systematic affiliation and have not been revised. l = leaf; d = diaspore, ls = leafy shoot; c = cone

leaves from the basaltic tuff at Kollnitz (Hofmann and Kahler, 1938). In the 1950s, Beck-Managetta (1952) and Berger (1955) discussed many of the previously known plant bearing localities of the Lavanttal Basin and reported on some newly discovered leaf-bearing sedimentary units. In addition to describing new specimens and localities, Berger (1955) also revised most of Hofmann's (1929) previously described taxa (Table 1). The ages of the leaf-bearing layers were determined as early to middle Miocene (Karpatian to Sarmatian). Knobloch (1977, 1981), Wank (1991) and Fritz (1998) described leaf, seed and fruit remains from Schönweg and St. Stephan, whilst Wank (1987, 1993) found more plant remains in lacustrine deposits at Fischering (between Wolfsberg and St. Andrä). Since 2005, the lacustrine part of the Mühldorf Formation, excavated by the Koralm-Tunnel project of the Austrian Railway (ÖBB) at the eastern margin of the Lavanttal Basin, has yielded numerous leaf remains with cuticles as well as fruit and fish remains (Meller and Kvaček, 2007).

3. Geological background of study area

The geology and stratigraphy of the Neogene Lavanttal Basin has been studied in detail (Figs. 1 and 2), initially by Beck-Mannagetta (1952), and later by Bassir (1964), Bechtel et al. (2007), and Reischenbacher et al. (2007), and most recently by Reischenbacher and Sachsenhofer (2013). The Lavanttal Basin is situated in the southern part of the Eastern Alps and, palaeogeographically, at the northwestern margin of the Central Paratethys. The basin formed as a pull-apart structure during dextral strike-slip movement, associated with lateral extrusion of the Eastern Alps, along the NNW-SSE striking Pöls-

	Upper Badenian			
Locality	Messensach	Hasenflüchter	St. Andrä	Siegelsdorf
Latitude and longitude (ca.)	46°44'50"N, 14°51'23"E	46°45'58"N, 14°49'25"E	46°45'58"N, 14°49'25"E	46°48'36"N, 14°47'45"E
Previously identified macrofloral elements	cf. *Castanea atavia* (l), *Populus latior* (l), ?cf. *Populus balsamoides* (l), cf. *Ulmus longifolia* (l), *Platanus aceroides* (l), *Cinnamomophyllum scheuchzeri* (l)	*Glyptostrobus europaeus* (ls), *Quercus drymeja* (l), *Quercus neriifolia* (l), *Cinnamomophyllum* cf. *polymorphum* (l)	*Carpinus* sp. (l), *Cinnamomum* sp. (l), *Dombeyopsis grandifolia* (l), *Fagus* sp (l).	*Cyperites canaliculatus* (l), *Phragmites oeningensis* (l), *Glyptostrobus europaeus* (ls), *Pinus hepios* (l), *Acer trilobatum* (l), *Alnus kefersteinii* (l), *Alnus* sp. (l), *Corylus insignis* (l), *Diospyros anceps* (l), *Fagus deucalionis* (l), *Myrica hakeaefolia* (l), *Myrica lignitum* (l), *Myrsine formosa* (l), *Podocarpus eocencica* var. *raxites* (l), *Pisonia eocenica* (l), *Quercus chlorophylla* vel *Q. daphnes* (l), *Quercus drymeja* et/ vel *Q. serra* (l), *Quercus* cf. *infectoria* (l), *Quercus daphnes* (l), *Quercus lonchitis* (l), *Quercus mediterranea* (l), *Rhamnus eridani* (l), *Rhamnus heerii* (l), *Salix varians* (l), *Sapindus falcifolius* (l), *Sapindus* sp. (l)
For geological background and plant fossils see	Berger 1955	Berger 1955	Zwanziger 1876	Zwanziger 1881, 1882; Hofmann 1929; Berger 1955
	Upper Badenian	**"Upper Badenian - Lower Sarmatian"**	**Lower Sarmatian**	**Upper Sarmatian**
Locality	Wolfsberg (Kohleschurf) and Hattendorf	Dachberg bei Jakling	St. Stefan (Bergbau)	Wolkersdorf
Latitude and longitude (ca.)	46°40'18"N, 14°56'59"E	46°39'16"N, 14°56'55"E	46°40'19N, 14°56'58"E	46°38'34"N, 14°56'26"E
Previously identified macrofloral elements	*Glyptostrobus europaeus* (ls, c), *Carpinus grandis* (l), *Cinnamomophyllum scheuchzeri* (l), *Ficus apocynoides* (l), *Myrica hakeaefolia* (l), *Myrica lignitum* (l), *Myrica* sp. (l), *Prunus* sp., *Quercus elaeana* (l), cf. *Quercus gmelini* (l), *Quercus lignitum* (l), *Salix chlorophylla* (l), *Salix macrophylla* (l), *Salix tenera* (l), *Salix varians* (l)	*Alnus kefersteinii* (l), *Carpinus grandis* (l), *Fagus deucalionis* (l)	*Glyptostrobus europaeus* (ls, c), *Callitris brongniarti* (ls), *Cupressites frenelopsis* (ls), *Stratiotes* (d), *Acer tricuspidatum* (l), *Büttneria aequalifolia* (l), *Cissus platanifolia* (l), *Platanus aceroides* (l), *Quercus parlatorii* (l), *Ulmus plurinervia* (l), *Ulmus* sp. (l)	*Osmunda* sp. (l), *Glyptostrobus europaeus* (ls, c), *Alnus* cf. *kefersteini* (l), *Büttneria aequalifolia* (l)
For geological background and plant fossils see	Zwanziger 1876, 1881; Hofmann 1929; Berger 1955	Zwanziger 1881; Hofmann 1929	Hofmann 1929; Knobloch 1977, 1981; Berger 1955	Berger 1955

Table 1: continued

Lavant fault system, during the early and middle Miocene. The Koralm fault system forms the eastern margin of the basin and has been active since the Badenian (Reischenbacher and Sachsenhofer, 2013).

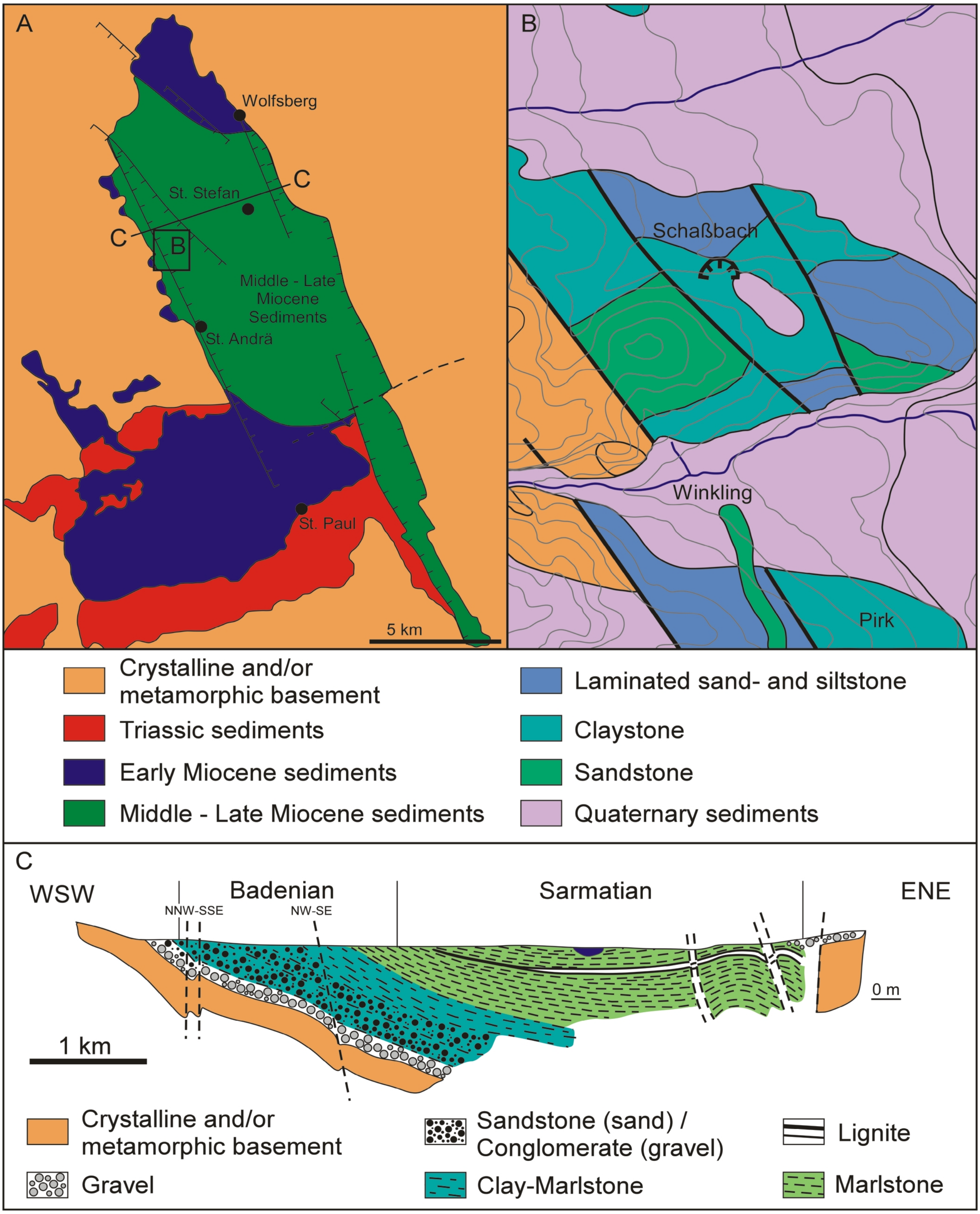


Figure 1: Simplified geological maps of the Lavanttal Basin (A) and of the area around the new fossiliferous locality. The Schaßbach locality (ca. 46°47'52"N, 14°48'20"E) is marked with a quarry icon (B). Schematic cross-section (C) shows the sedimentary units within the Lavanttal Basin (modified after Beck-Mannagetta, 1952; Weissenbach and Pistotnik, 2000; Bechtel et al., 2007; Reischenbacher et al., 2007).

The oldest Cenozoic sediments in the basin, from the latest early Miocene (Karpatian, Burdigalian; ca. 17-16 Ma), are fluvial deposits of the Granitztal Beds. These overlie crystalline basement and adjacent Mesozoic sediments (Figs. 1 and 2). The Granitztal Beds are succeeded by lower Badenian (ca. 16-14.5 Ma) sediments of the Mühldorf Formation, which is divided into an older non-marine fish shale unit and a younger marine sequence (Fig. 2). The age of this formation is based on various combined biostratigraphic proxies and chronostratigraphic and biostratigraphic correlations (e.g. Beck-Mannagetta, 1952; Weinfurter, 1952; Berger, 1955; Kühn, 1963; Schmid, 1974, Meller and Kvaček, 2007; Reischenbacher et al., 2007; Reischenbacher and Sachsenhofer, 2013), and absolute age determinations of ca. 14.9 Ma from volcanic units within the formation (Lippolt et al., 1975). The sediments overlying the Mühldorf Formation, from the middle Badenian, are of marine origin, but fossils encountered in successively younger units indicate a gradual shift to brackish environments and finally freshwater conditions during the late Badenian. Sediments of freshwater and brackish origin, with conspicuous lignite horizons (coal seams), continued to accumulate during the Sarmatian (ca. 12.7-11.6 Ma) and early Pannonian (e.g. Beck-Mannagetta, 1952; Bechtel et al., 2007; Reischenbacher et al., 2007; Reischenbacher and Sachsenhofer, 2013).

The Schaßbach locality (district of Oberaigen) is situated at the western margin in the central part of the Lavanttal Basin, yielding sediments considered to be of early Badenian age (Figs. 1 and 2). The outcrop is an active clay-pit, continuously producing fresh sediments and fossil material. The sediments consist mainly of silty mica-bearing clays or clayey silts of grey to bright brown colour. Thin grey-brown flexible clay layers ("Papierschiefer") are intercalated. Several layers contain, together with plant remains, poorly preserved ostracoda shells that are smooth and thin in macroscopic view. This sediment type is comparable to that described by Zwanziger (1881, 1882) from Siegelsdorf (N Schaßbach), also considered of Badenian age (Beck-Mannagetta, 1952; Berger, 1955).

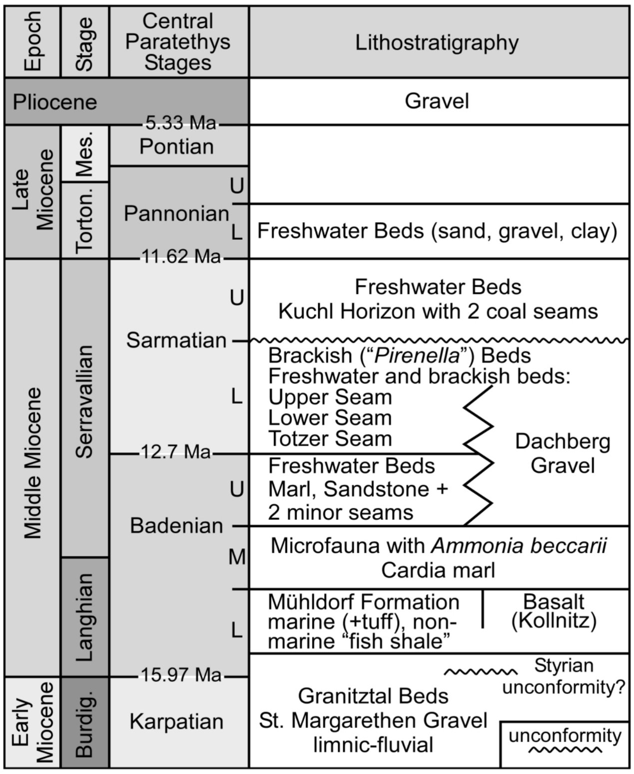


Figure 2: Generalized stratigraphy of the Lavanttal Basin (modified after Beck-Mannagetta, 1952; Tollmann, 1985; Reischenbacher and Sachsenhofer, 2013).

The age of the sediments at Schaßbach is based on the following evidences: (1) the geographic position of the outcrop within the Lavanttal Basin: Regional stratigraphy and the dip of the strata (see figure 1 in Reischenbacher and Sachsenhofer, 2013) suggest that surface exposures in this area belong to lacustrine and/or marine sediments of early Badenian age. (2) The sedimentary sequence with the plant fossil locality also contains the typical "non-marine fish shale" that is unique to the lower part of the Mühldorf Formation within the Lavanttal Basin (authors observations). (3) Fish remains from this locality suggest they belong to at least three different taxa, *Gobius* and *Leuciscus*, which are mostly freshwater types, and *Morone*, which lives in brackish environments but spawns in freshwater. All three "freshwater" taxa are characteristic of the "fish shale" of the Mühldorf Formation (e.g., Beck-Mannagetta, 1952; Wank, 1991; Kandutsch and Molterer, 2014). However, the fish layers near Mühldorf contain more sulphur than the layers at Schaßbach, indicating a more marine or brackish dominated influence at Mühldorf (Kandutsch and Molterer, 2014). (4) Preliminary studies on molluscs from the locality also indicate the presence of gastropods similar to those mentioned by Beck-Mannagetta (1952) being characteristic for freshwater environments and confined to the Mühldorf Formation.

4. Material and Methods

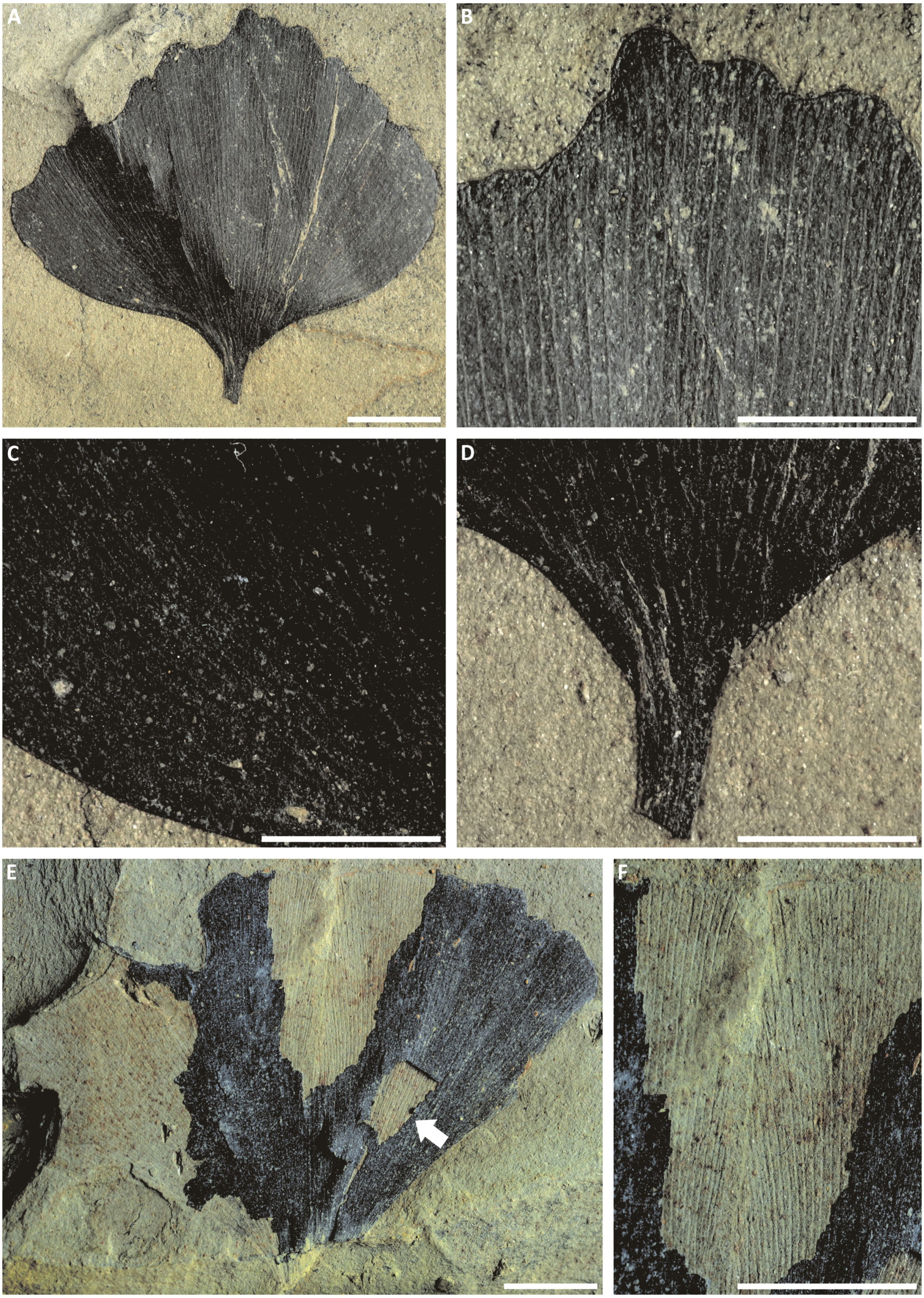
The fossils presented here were collected during the last few years. Fossils and sediment samples are stored in the collection of the Department of Palaeontology, University of Vienna. Additional material was collected by private collectors and is kept in private collections.

Leaf foliage was generally described using the accepted terms for Ginkgophyte foliage remains. The macroscopic pictures of *Ginkgo* leaves were taken using a Nikon D800 digital camera. The cuticle fragments were macerated using Danclor™ solution for 24 hours. The cuticles were then rinsed with water and transferred into glycerine. For light microscopy observations, cuticles were stained with red safranin and then photographed with a Nikon Eclipse 80i microscope.

5. Results

5.1 Systematic palaeontology

Division Ginkgophyta
Family Ginkgoaceae Engler
Genus *Ginkgo* Linné
Species *Ginkgo adiantoides* (Unger) Heer, (Figures 3-5)


A
B
C
D
E
F

1845 *Salisburia adiantoides* Unger – Unger, p. 211 (late Miocene, Italy).
1850 *Salisburia adiantoides* Unger – Unger, p. 392 (late Miocene, Italy).
1859 *Salisburia adiantoides* Unger – Massalongo & Scarabelli, p. 163-165, pl. 1, fig. 1, pl. 6, fig. 18, pl. 7, fig. 2, pl. 39, fig. 12 (late Miocene, Italy).
1878 *Ginkgo adiantoides* Unger – Heer, p. 21-22, pl. 2, figs. 7-10 (Miocene, Sachalin).
1933 *Ginkgo* sp. (aff. *biloba* L.) – Gothan & Sapper, p. 5, pl. 2, fig. 12 (middle and late Miocene, Germany).
1936 *Ginkgo adiantoides* (Unger) Heer emend. Florin – Florin, p. 29-30, pl. 2, figs. 3-9 (Pliocene, Germany).
1939 *Ginkgo adiantoides* (Unger) Heer – Mädler, p. 46-48, pl. 5, figs 1-4 (Pliocene, Germany).
1955 *Ginkgo adiantoides* (Heer) Engelh. & Kink. – Berger, p. 84-85, figs. 3-5 (late Miocene, Austria).
1959 *Ginkgo adiantoides* (Unger) Heer – Andreánszky, p. 48-49, pl. 7, fig. 8, pl. 8, figs. 2 & 5 (late middle Miocene / Sarmatian, Hungary).
1959 *Ginkgo adiantoides* (Unger) Heer – Kovács-E. in Andreánszky, p. 222-224 (middle Miocene, Hungary).
1964 *Ginkgo adiantoides* (Unger) Heer – Mai, p. 9-10 (latest early Miocene, Germany).
1984 *Ginkgo adiantoides* (Unger) Heer – Kordos-Szakály, p. 47 (middle Miocene / Badenian, Hungary).
1988 *Ginkgo adantoides* (Unger) Heer – Kovar-Eder, p. 26-27, pl. 1, Figs. 1-3 (late Miocene, Austria).
1994 *Ginkgo adiantoides* (Unger) Heer – Kvaček et al., pl. 1, figs. 1-2 (Pliocene, Hungary).
1997 *Ginkgo adiantoides* (Unger) Heer – Hably & Kvaček, p. 12-13, pl. 1, figs. 1-4, pl. 2, figs. 5-6, pl. 3, figs 7-8 (Pliocene, Hungary).
1998 *Ginkgo adiantoides* (Unger) Heer – Hably & Kvaček, pl. 1, fig. 1, text-figs. 2/1, 3/1 (Pliocene, Hungary).
2000 *Ginkgo adiantoides* Heer – Seehuber, p. 283 (late middle Miocene/ Sarmatian, S-Germany).
2002 *Ginkgo adiantoides* (Unger) Heer – Nemejc et al., p. 129, pl. 4, figs. 1-3, pl. 9, figs. 6-7 (middle Miocene, Czech Republic).
2002 *Ginkgo adiantoides* (Unger) Heer – Denk & Velitzelos, p. 3-6, pl. 1, figs. 1-2, pl. 2 (late Miocene, Greece).
2007 *Ginkgo adiantoides* (Unger) Heer – Hably & Fernandez Marrón, p. 68, fig. 2 (late Miocene, Spain)
2010 *Ginkgo adiantoides* (Unger) Heer – Walther & Eichler, p. 197-198, pl. 1, fig. 10, pl. 8, fig. 1 (late Miocene, Germany).
2014 *Ginkgo adiantoides* (Unger 1845) Heer 1874 – Gregor et al., p. 9-10, pl. 8, figs. 1-2 (Miocene, Pliocene, Germany).

Material: Two leaves, one missing part of the petiole (Fig. 3A-D; Andreas Hassler, St. Andrä pers. collection; spec. no. SH033), the other missing the proximal part of the lamina and petiole (University of Vienna, Department of Palaeontology, IPUW 7403/1). Both leaves have cuticles preserved.

Description gross morphology: Leaves with petiole (Fig. 3A), preserved part of petiole up to ca. 9 mm long, and up to 4 mm wide (Fig. 3B); the lamina is 35 to 46 mm long and 46 to 62 mm wide; lamina is strongly obovate in shape, fan-like, with a cuneate decurrent base (Fig. 3A, E), lateral margins straight to slightly concave, distal margin undulate; veins originate at the base (Fig. 3D), veins parallel arranged (Fig. 3B, F), veins forking several times towards the margin (Fig. 3C, F), 19 to 24 veins ending per 1 cm distal margin (Fig. 3B, F) and also in the middle part of the lamina.

Description abaxial (lower) cuticle: Cells over veins elongated (Fig. 4A-C, D), cells 70-160 µm long and 30-50 µm wide, cells with acute to rectangular ends, anticlinal cell walls mostly straight (Fig. 4C, E), rarely slightly undulate; cells of intercostals areas rectangular to polygonal or irregular in outline (Fig. 4A, C, F), cells 30-150 µm across, often papillate; stomata 20-35 µm long, subsidiary cells complete or incomplete amphicyclocytic, subsidiary cells often papillate (Figs. 4G, H, 5A-D).

Description adaxial (upper) cuticle: Cells over veins elongated (Fig. 5E, G), cells 80-150 µm long and 20-40 µm wide, cells with acute and rarely rectangular ends, anticlinal cell walls undulate; cells of intercostals areas triangular to polygonal or isodiometric in outline (Figs. 5E-H), cells 50-100 µm across, anticlinal cell walls undulate; no stomata or papillae present.

Remarks: The macromorphological features of the lamina fits well with those of *Ginkgo adiantoides* originally reported as *Salisburia* from the late Miocene of Italy (Unger, 1845, 1850; Massalongo and Scarabelli, 1859) and other *Ginkgo* leaf remains later affiliated to *G. adiantoides* from various late Miocene to Pliocene localities in Europe (see synonym list above and table 1 in Denk and Velitzelos, 2002). Only the number of veins per 1 cm margin is slightly higher than counted in most other *Ginkgo* remains (c.f. table 2 in Denk and Velitzelos, 2002). *Ginkgo* leaf fossils (impressions) from the few other Austrian late Miocene localities of Laaerberg (Berger, 1955), Großenreith, Lohnsburg, and Stegersbach (Kovar-Eder, 1988), also fit very well in gross morphology to the new specimens described here from Schaßbach apart from their slightly larger dimensions (lamina up to 60 mm wide, petiole up to 55 mm preserved). They also have the undulate distal margin in common, without any deep incisions.

The epidermal features of the Lavanttal leaf fossils are also corresponding to that of *G. adiantoides* from the late Miocene of Vegora, Greece, as described/figured by Denk and Velitzelos (2002). Slight differences occur in the dimensions of the

Figure 3: *Ginkgo adiantoides* leaf fossils from Schaßbach, Lavanttal Basin (early Badenian). A-D. *Ginkgo adiantoides* foliage with all the organic material preserved (A. Hassler, St. Andrä pers. collection; spec. no. SH033). A. Foliage, part of the petiole missing. B. Close-up showing venation along margin and undulate margin. C. Close-up showing forking of veins in lateral part of lamina. D. Close up showing proximal part of leaf, part of the petiole, and origin of veins. E-F. *Ginkgo adiantoides* foliage with parts of the organic material preserved (University of Vienna, Department of Palaeontology, IPUW 7403/1). E. Foliage, part of the proximal part missing, cuticula sample area indicated by arrow. F. Close-up showing the parallel venation and forking towards margin. Scale bar 1 cm in A and E, and 5 mm in B-D and F.

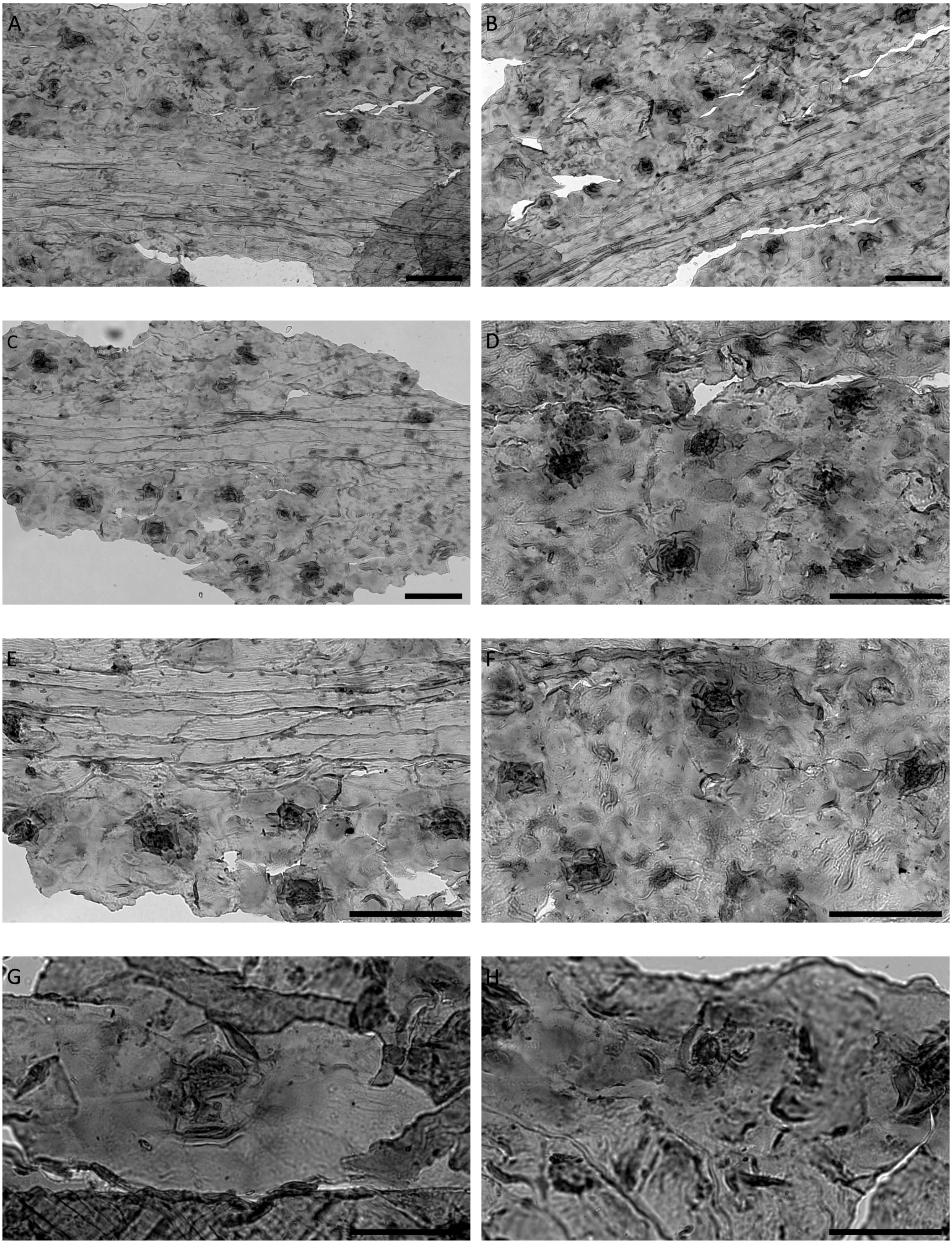


Figure 4: Cuticles of *Ginkgo adiantoides* leaf fossil from Schaßbach, Lavanttal Basin (early Badenian). A-H. Abaxial (lower) cuticle fragments (University of Vienna, Department of Palaeontology, IPUW 7403/1. A-C, E. Cuticle with elongate cells over veins, and polygonal to irregular outlined cells and stomata with subsidiary cells in intercostals areas. D, F. Cuticle from intercostal areas showing rectangular to polygonal or irregular cells, cells and stomata often papillate. G, H. Close-ups of intercostal areas showing stomata and amphicyclocytic subsidiary cells. Scale bar 50 µm in G and H, and 100 µm in A-F.

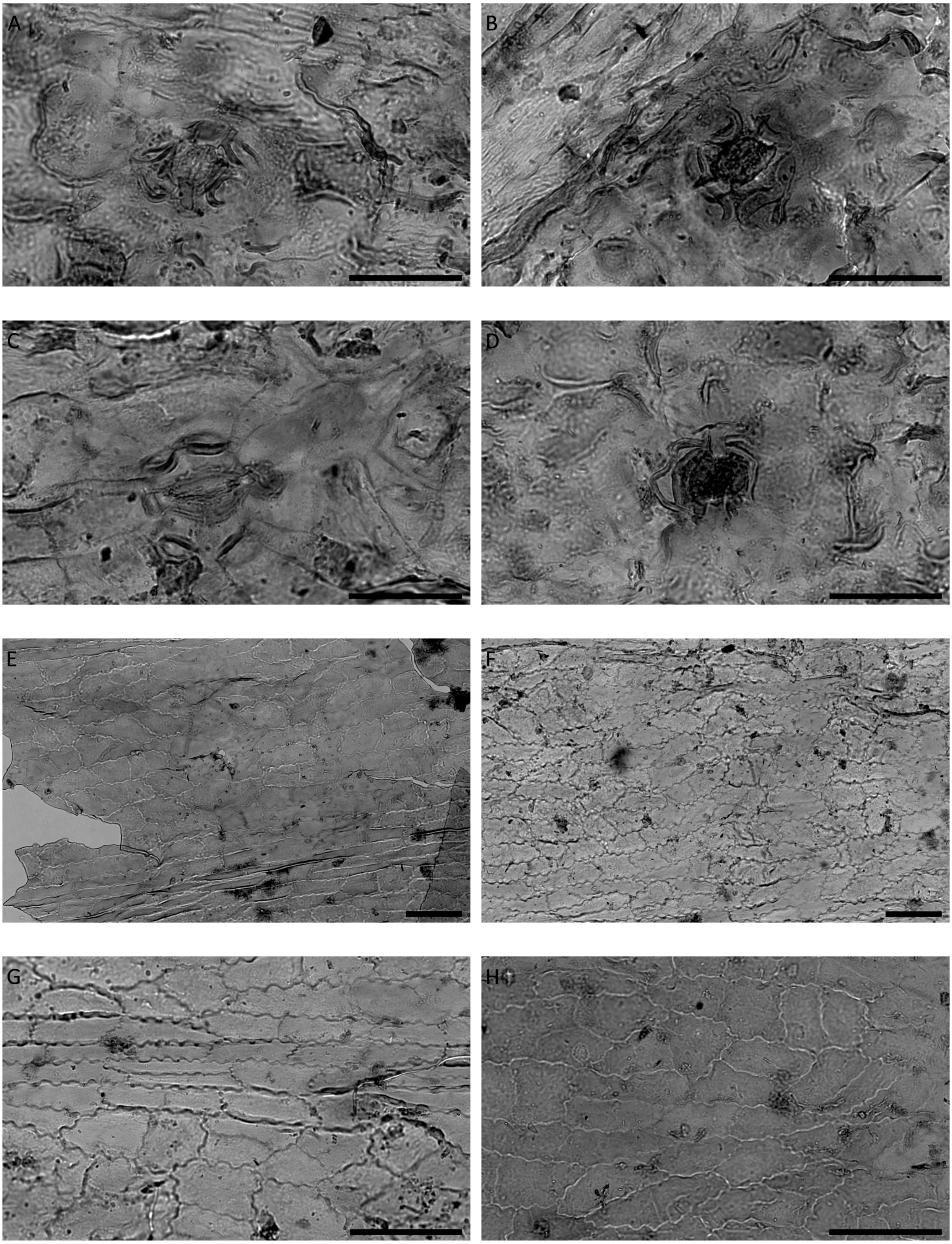


Figure 5: Cuticles of *Ginkgo adiantoides* leaf fossils from Schaßbach, Lavanttal Basin (early Badenian). A-D. Abaxial (lower) cuticle fragments. E-H. Adaxial (upper) cuticle fragments (University of Vienna, Department of Palaeontology, IPUW 7403/1. A-D. Close-ups of intercostal areas showing stomata and amphicyclocytic subsidiary cells, subsidiary cells often papillate. E, G. Cuticle with elongate cells over veins, and triangular to polygonal or isodiometric outlined cells in intercostals areas. F, H. Cuticle with triangular to polygonal or isodiometric outlined cells in intercostals areas, anticlinal cell walls undulate. Scale bar 50 µm in A-D, and 100 µm in E-H.

abaxial epidermal cells over veins in the leaf remains from Vegora and longer cells occur in the *Ginkgo* leaf cuticles from Frankfurt (c.f. Denk and Velitzelos, 2002).

6. Discussion

6.1 Cenozoic records of *Ginkgo* in the Northern Hemisphere

Ginkgophytes first appeared in the late Paleozoic and became most diverse during the Mesozoic. Zhou (2009) proposed that Laurasia was the place of origin because of the numerous records there. Several studies show a close relationship between *Ginkgo biloba* L. and the Coniferales, Gnetales and Cordaitales, whereas the relationship with the Cycadales is less well supported (Taylor et al., 2009). The genus *Ginkgo*, which has existed since the Jurassic, is the only Ginkgoaceae genus that probably survived the Mesozoic-Cenozoic transition. During the Cenozoic, *Ginkgo* was widely distributed in the Northern Hemisphere, but has rarely been documented from the Southern Hemisphere. Up to 18 different *Ginkgo* species have been described from the Cenozoic (Zhou, 2009), mainly based on leaf remains (e.g., Samylina, 1967; Tralau, 1968; Samylina and Chelebayeva, 1986; Denk and Velitzelos, 2002; Quan et al., 2010) and rarely on wood (Zhou, 2009; Mustoe, 2002). *Ginkgo* seeds are almost entirely missing from Cenozoic localities of Europe; Mädler (1939) mentioned seed remains from the Pliocene of Frankfurt and Gregor (1992) from the Pliocene of Kaltenhausen (France). The seeds from Frankfurt are doubtful and the original specimens have been lost according to Gregor (1992). Fossil *Ginkgo* pollen can only be correctly identified using SEM (e.g. Grímsson et al., 2011). Thus all European Cenozoic *Ginkgo* pollen records based solely on light microscopy are considered to be questionable. *Ginkgo* pollen grains documented using a combination of LM and SEM have not been reported from any Central European Paleocene to Eocene localities. From the Oligocene, there exists only a single European *Ginkgo* pollen record based on SEM, from Bockwitz, Germany (see Gastaldo et al., 1998). Additional SEM based identifications from Europe are mostly from the middle and late Miocene, a time when *Ginkgo* apparently became more frequent in European forests, and also from Pliocene sediments (e.g. Grímsson et al., 2011; author's personal observation). Tralau (1968) questioned the validity of all the different *Ginkgo* species and suggested that most Cenozoic leaf remains might represent a single species, *G. adiantoides*. Tralau (1968) also considered whether *G. adiantoides* was identical to the extant *G. biloba*. New Ginkgoaceae findings from the Paleocene of China are believed to represent two co-occurring species, *G. adiantoides* and *Ginkgo jiayiensis* C. Quan, G. Sun, & Z. Zhou (Quan et al., 2010). From the Eocene of western North America two contemporaneous species have also been described, *Ginkgo dissecta* Mustoe and *G. biloba* (Mustoe, 2002). The leaf morphology of *Ginkgo jiayiensis* is similar to those of *G. adiantoides* and *G. biloba*, but the upper and lower cuticles have numerous stomata on both sides. Amphistomatic leaves are characteristic for *G. biloba*, but with only rare stomata on the abaxial cuticle. *Ginkgo dissecta* leaves differ strongly in their morphology by their multilobate lamina, and are similar in gross morphology to Mesozoic *Ginkgo* foliage remains. This suggests that during the Paleogene *Ginkgo* was more diverse than in Neogene times.

The Cenozoic history of *Ginkgo* seems to be quite variable in different geographical regions; North America vs. northern North Atlantic realm vs. continental Europe vs. Asia (e.g., Tralau, 1968; Denk and Velitzelos, 2002). During the Cenozoic of mainland Europe (excluding the Greenland – Iceland - Faeroe Islands - British Isles - Svalbard area), fossil *Ginkgo* records are of Miocene to Pliocene age and it is likely that all the Neogene European leaf macrofossil findings of genus *Ginkgo* belong to the same fossil taxon, *Ginkgo adiantoides* (Ung.) Heer (e.g. Denk and Velitzelos, 2002).

Ginkgo leaves of the *G. adiantiodes* type apparently did not occur in Central Europe prior to the latest early Miocene as shown by the *Ginkgo* foliage fossils from Wiesa, Germany, (Kabusch, 1954; Mai, 1964) and Schaßbach, Austria, (this study). However, the alleged latest early Miocene records from Wiesa were not properly described and were only figured in a local report by Kabusch (1954). Furthermore, it is not known from which sedimentary units in Wiesa the leaf fossils were collected. Therefore their precise age and stratigraphic position is uncertain (e.g. Kabusch, 1954; Mai, 1964). Other European *Ginkgo* records are considered slightly younger, e.g. from the late Badenian site at Nógrádszakál, in Hungary (Kordos-Szakály, 1984).

During the middle Miocene and up to the Pliocene, *Ginkgo* apparently became a common accessory element (compare synonym list above) within the deciduous forests of mainland Europe. Note the occurrence of *Ginkgo* contemporaneous with the Middle Miocene Climatic Optimum and that the Hungarian locality (Nógrádszakál) is characterised by more temperate elements than in younger Sarmatian leaf assemblages (e.g. Erdei et al., 2007). Kovar-Eder et al. (1994) regarded the Hungarian late Badenian *Ginkgo* record as the oldest for the Central Paratethys and concluded that it arrived at the same time as *Acer vindobonensis* (Ettingshausen) Berger and *Alnus ducalis* (C.T. Gaudin) Knobloch. Based on this study, *Ginkgo* adiantoides was already thriving in the Central Parathetys area during the early Badenian, along with *Platanus leucophylla* (Unger) Knobloch and *Acer quercifolia* (Göppert) Kovar-Eder; both are in the Schaßbach flora (author's work in progress). It is likely that the fossil *Ginkgo* pollen reported by Grímsson et al. (2011) from the Sarmatian of the Lavanttal Basin belong to the same biological species as the foliage from the older Badenian sediments of the Schaßbach locality. This suggests that *Ginkgo* thrived in the Lavanttal area for at least 4 million years, from early Badenian times until the late Sarmatian.

5.2 The Schaßbach *Ginkgo* remains and their ecological implications

At present, *Ginkgo* is a relict genus with only a single living species, *Ginkgo biloba* L., and it is often called a living fossil. Modern *Ginkgo* trees are deciduous and up to about 30 m high. In the past, *Ginkgo* was often cultivated near temples in China, Korea and Japan, and natural habitats were not known or considered doubtful (e.g., He et al., 1997; Raven et al., 1999). The occurrence of *Ginkgo* within the Tianmu mountains (Tianmushan) was used to propose that that area was a natural habitat (Del Tredici, 1992). However, analysis of isoenzymes showed a low genetic variation, indicating that the population evolved from cultivated individuals (Schütt et al., 2004). Recent investigations (Gong et al. 2008, cf. Del Tredici, 2007) confirmed two refuge areas where *Ginkgo* apparently survived during the Pleistocene; Jinfo Mountains, Chongqing Province, SW China, and the west Tianmu Mountains in East China. According to Tang et al. (2012), these and other occurrences are still not convincing as natural stands. The investigations of Tang et al. (2013) on *G. biloba* populations in the Dalou Mountains of SW China suggest that those are the only populations that can be considered fully natural. These populations are characterized by three types of *Ginkgo* plant communities; 1. *Ginkgo* dominated, 2. *Ginkgo* and *Cupressus funebris* Endl. dominated, 3. dominated equally by *G. biloba*, *Liquidambar formosana* Hance, *Cyclobalanopsis glauca* (Thunb.) Oerst., *Cunninghamia lanceolata* (Lamb.) Hook., *Taxus wallichiana* var. *chinensis* (Pilger.) Florin. There are convincing occurrence of other relict species within these forests, such as *Metasequoia glyptostroboides* Hu et Cheng, *Davidia involucrata* Baill., and *Cathaya argyrophylla* Chun et Kuang, *Cercidiphyllum japonicum* var. *sinense* Rehder et E. H. Wilson, *Tetracentron sinense* Oliv., and *Liriodendron chinense* (Hemsley) Sargent. Many of these floral elements are typical of the Miocene forests in Europe (e.g. Mai, 1995).

Modern *Ginkgo* trees grow mostly in lowland regions, valleys and on mountain slopes, at elevations between 300-1100 m, along the Yangtze River (Flora of China Editorial Committee, 1999). Del Tredici et al. (1992) noted that *Ginkgo* trees grow mostly in disturbed micro-habitats, along streams and rivers, on steep rocky substrates, and at the edge of cliffs. It has also been suggested that the trees are gap opportunists and can thrive well as understory elements until they become canopy trees (Del Tredici, 1989). The population of the Dalou Mountains now occurs between 840 and 1200 m altitude on soils developed from limestones, but the original population is assumed to have grown there along valleys and lower mountain slopes (Tang et al., 2012).

Many of the macrofloral elements occurring at Schaßbach are represented by numerous specimens (e.g., *Acer*, Betulaceae, Fagaceae, *Glyptostrobus*, *Platanus* and *Zelkova*) suggesting that these remains originate from plants growing in close vicinity to the sedimentary basin. These typical and frequently occurring elements reflect parts of the azonal vegetation thriving in lowland wetlands along/at the margin of the palaeolake during the early Badenian in Lavanttal. In contrast, some macrofossil remains, like the *Ginkgo* leaves, are extremely rare at Schaßbach, and are only represented by a single or few fragmentary specimens. These are considered to reflect parts of the azonal riparian vegetation that were transported into the lake via streams and rivers. A similar scenario has been proposed by Royer et al. (2003) for the genus *Ginkgo* during the Late Cretaceous to middle Miocene, suggesting that *Ginkgo* trees were mostly growing in disturbed areas, along streams and rivers and on natural levees. This suggests that the *Ginkgo* of the Lavanttal Basin was growing outside the main sedimentation zone, thriving along streams and rivers running into the basin, and dispersing into newly opened microhabitats such as river banks and floodplain margins. These conclusions corroborate observations from Unterwohlbach (South Germany, Butzmann and Fischer, 1997, Seehuber, 2000), one of the rare localities where *G. adiantoides* records are abundant. A floristic comparison of Unterwohlbach with modern forests in China showed that more than 70 % of the genera documented at Unterwohlbach are also found in the Mixed Mesophytic Forests of the lower and upper Yangtze River in China (Wang, 1961). At Unterwohlbach *Ulmus*, *Salix*, *Populus*, are very abundant, whilst *Ginkgo*, *Zelkova*, *Platanus*, *Fabaceae*, *Juglans*, *Cinnamomum*, and *Celtis* are abundant.

It is difficult to extract any climate signal based solely on the *Ginkgo* remains since it is apparent that modern day *Ginkgo* has a much more restricted distribution than its predecessors during most of the Cenozoic, suggesting that it may have had a wider ecological range than at present. The modern distribution may reflect only part of the ecological/climate range of the genus during most of the Paleogene and Neogene. Still, Fang et al. (2009) reported that *Ginkgo biloba* trees in China (including cultivated ones) thrive under warm humid climates with mean annual temperatures (MAT) of 6.2-(15.6)-21.8°C and an annual precipitation of 428-(1295)-1997 mm. The climate of the Dalou Mountains, situated between Chongqing and Guizhou Province, is also described as subtropical, warm and humid. For the Jinfo Mountains, Chongqing province, 16.6°C MAT and 1185 mm mean annual precipitation (MAP) are mentioned (Del Trededi, 2007), for the Tian Mu Shan Reserve, 8.7°C and 1767 mm at 1506 m above sea level and 14.9°C MAT, 1536 mm MAP at 350 m above sea level are cited (Del Tredici, 1992). The present "natural" distribution of *Ginkgo* in China occurs under a typical Cfa climate (warm temperate, fully humid, hot summers, maximum mean monthly temperature ≥ +22°C), but where it has been naturalized after cultivation in Asia and Europe, *Ginkgo* also thrives and bears fruits in Cfb climate (warm temperate, fully humid, warm summer, at least 4 months with mean monthly temperature of ≥ +10° C) without problems (for a more detailed explanation of Cfa, Cfb and other climate types see Kottek et al., 2006). Based on the late Cenozoic fossil record of *Ginkgo adiantoides* (see synonym list above) it is even likely that a Cfb climate was the preferred niche of the genus before it came under threat of extinction, and it is now only growing "naturally" in a restricted area under Cfa climate. The few remains of *Ginkgo adiantoides* leaves from the Lavanttal and Wiesa (the type locality of the Mastixioideae-floras, Mai, 1964) might indicate that the climate conditions around the MMCO were not ideal for the distribution of *Ginkgo*. Only following a slight cooling, did *Ginkgo* became more common.

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Barbara MELLER[1)], Reinhard ZETTER[1)], Andreas HASSLER[2)], Johannes M. BOUCHAL[1)], Christa-Charlotte HOFMANN[1)] & Friðgeir GRÍMSSON[1)*)]

[1)] University of Vienna, Department of Paleontology, Althanstraße 14 (UZA II), A-1090 Vienna, Austria;

[2)] Burgstall-St.Andrä 99, 9433 St. Andrä, Austria;

[*)] Corresponding author, fridgeir.grimsson@univie.ac.at

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