The leaf assemblage from the Early – Middle Miocene locality Sulzigtobel near Werthenstein (Canton Lucerne, Switzerland)

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Abstract. A first taxonomic overview on the moderately diverse Early – Middle Miocene (Burdigalian-Langhian) leaf assemblage from the locality Sulzigtobel near Werthenstein (Canton Lucerne, Switzerland) is provided. The leaves originate from marly-silty pond sediments intercalated between massive conglomerates of the Napf alluvial fan delta of the Upper Freshwater Molasse. The flora is dominated by leaves of Daphnogenes polymorpha, Populus cf. zaddachii and a so far unidentified taxon, provisionally named Dicotylophyllum sp. A. Additional taxa with only a few or single records are: cf. Lygodium kaulfussii, Smilax sp., Poaceae vel Cyperaceae gen. et sp. indet., Typha sp., Comptonia sp. vel Myrica oehningensis, Myrica cf. lignitum, Berchemia multinervis, cf. Thevetia sophiae, cf. Salix sp., cf. Acer tricuspidatum, Dicotylophyllum sp. B, and Dicotylophyllum sp. C. Most of these taxa probably grew in riparian habitats on the dynamic landscape on top of the Napf alluvial fan delta.

Key words: flora, leaves, Miocene, Switzerland, Northern Alpine Foreland Basin, Upper Freshwater Molasse, Sulzigtobel

Introduction

The Northern Alpine Foreland Basin (NAFB) is famous for its wealth of fossil bearing localities from the Late Palaeogene and Neogene. Besides remains of mammals and other vertebrates as well as invertebrates (e.g. Sach 2014), fossil plants are known from a large number of localities (e.g. Mai 1995; Sach 2014). The western part of the NAFB located in Switzerland and Southern Germany is regarded by many palaeobotanists as one of the ‘classic’ regions of Tertiary palaeobotany ever since the publication of Oswald Heer’s monumental monograph ‘Flora Tertiara Helvetiae’ (Heer 1855, 1865, 1859). During the last century several new plant bearing localities were discovered (e.g. Hantke 1982, 1984; Büchler 1990) and these, together with in depth research on long known localities (e.g. Hantke 1954; Nötzold 1957; Uhl & al. 2003, 2006; Teodoridis & Kvaček 2005), enlarged our knowledge about palaeofloras and -climates of this region considerably.

This contribution provides a first overview on the Miocene leaf assemblage from the locality Sulzigtobel near Werthenstein (Canton Lucerne, Switzerland) which has not been studied in detail so far, together with first palaeoecological and taphonomic interpretations.

Geology and stratigraphy

The locality Sulzigtobel (Canton Lucerne, Switzerland; Fig. 1) is located in the eastern part of the Miocene Napf alluvial fan, approximately 1000 m south of the town of Werthenstein in a cliff at the so called ‘Sulzigbachfall’ (a waterfall of the small creek Sulzigbach; Fig. 2).
The plant bearing horizon consists of fluvially deposited, grey marls and siltstones which reach a thickness of up to 1.5 m. This horizon is sandwiched between two massive conglomerate beds (Figs 3, 4).

The exact lateral extension of the horizon is unknown, as its westernmost part is completely covered with slope debris (Fig. 4 C). On its eastern side it is flanked by a channel-like structure (Fig. 4 A) also filled with marls and siltstones.

Fig. 1. Map of Switzerland showing the position of the locality Sulzigtobel near Werthenstein (star).

Fig. 2. Map of the vicinity of Werthenstein near Lucerne, indicating the position of the locality Sulzigtobel at the ‘Sulzibachfall’ (arrow).

Fig. 3. Lithological profile of the locality Sulzigtobel. The plant-bearing horizon is marked by the leaf symbol.
Lithologically the horizon belongs to the mostly coarse-clastic sediments of the Napf alluvial fan of the Upper Freshwater Molasse of the NAFB. Based on remains of small mammals, the nearby locality Wolhusen-Grabenhüsli has biostratigraphically been dated as belonging into mammal zone MN 5 (Kärpatian-Badenian [Burdigalian-Langhian respectively]; Kälin & Kempf 2009). Lithological correlation suggests that the Sulzigtobel locality is located approximately 40 m above the locality Wolhusen-Grabenhüsli, which lies approximately 2 km southwest of the Sulzigtobel locality. This implies that the Sulzigtobel is only slightly younger than this locality and that we are probably still within mammal zone MN 5 (Paul Felber, Fällanden/Switzerland, written comm. 2009).

Material and methods

Material
The present study is based on approximately 1500, mostly fragmentary, leaf remains stored in the collections of the Natural History Museum in Lucerne (Inv.-Nr. ST 69-001 – ST 69-357) and the Institute of Geology at the ETH Zurich (Inv.-Nr. ETHZ 42, 01, xx/xx) in Switzerland. The material was collected by the late Swiss palaeobotanist Otto Appert between 1955 and 1973 (O. Appert, pers. comm, 2009).

Methods
Leaves were investigated with aid of a Leica M 80 binocular microscope. Photographs of leaves were taken with a Canon Powershot G11 camera. Contrast and brightness of the images were adjusted with Corel Photopaint X4.

Fossil cuticles were successfully extracted from freshly collected specimens in the late 1950ies by O. Appert and could be analysed for the purpose of this study. However, parts of the slides made by O. Appert were damaged during storage due to desiccation of the embedding agent glycerine-gelatine. Later attempts of cuticle extraction unfortunately failed due to oxidation and desiccation of the cuticle remains on the carbonized material during storage.

The flora
Ferns
A single fragmentary remain of the basal part of a leaf can be compared to the schizeaceous fern *Lygodium kaulfussii* Heer 1861 (Fig. 5 A). The specimen exhibits a dichotomous venation pattern typical for sterile pinnales of this taxon. Leaves of the genus *Ginkgo* exhibit a very similar fan-shaped venation pattern, although having a rather acuminate leaf base with narrow venation. It further seems that the fossil of Sulzigtobel possesses two prominent main veins closely resembling the pseudomonopodial growth form of *Lygodium*.
Fig. 5. Leaves from the Miocene locality Sulzigtobel near Werthenstein (Switzerland): A) Leaf fragment of *Lygodium kaulfussii* Heer; scale bar = 1 cm; Inv.-Nr. ETHZ 42, 01, 09/35; B) Leaf of *Smilax* sp.; scale bar = 1 cm; Inv.-Nr. ETHZ 42, 01, 03/15/35; C) Leaf of *Smilax* sp.; scale bar = 1 cm; Inv.-Nr. ETHZ 42, 01, 07/5; D) cf. *Typha* sp.; scale bar = 1 cm; Inv.-Nr. ETHZ 42, 01, 12/7; E) cf. *Typha* sp.; scale bar = 1 cm; Inv.-Nr. ETHZ 42, 01, 12/7; F) Poaceae vel Cyperaceae gen. et sp. indet.; scale bar = 1 cm; Inv.-Nr. ETHZ 42, 01, 01/2; G) *Daphnogene polymorpha* (A. Braun) Ettingsh.; scale bar = 1 cm; Inv.-Nr. ETHZ 42, 01, 01/1; H) *Daphnogene polymorpha* (A. Braun) Ettingsh.; scale bar = 1 cm; Inv.-Nr. ETHZ 42, 01, 01/1; I) *Daphnogene polymorpha* (A. Braun) Ettingsh.; scale bar = 1 cm; Inv.-Nr. ETHZ 42, 01, 01/1; J) *Daphnogene polymorpha* (A. Braun) Ettingsh.; scale bar = 1 cm; Inv.-Nr. ETHZ 42, 01, 01/1; K) *Daphnogene polymorpha* (A. Braun) Ettingsh.; scale bar = 1 cm; Inv.-Nr. ETHZ 42, 01, 12/10.
Most fossil records of L. kaulfussii refer to a description by Heer (in Heer & Andrae 1861) from a sterile specimen of the Early Oligocene locality Schkopau (Sachsen-Anhalt, Germany). A fossil exhibiting the adnation of both, sterile and fertile leaves of Lycopodium, was found in the late Eocene locality of Wyoming (Manchester & Zavada 1987). It is precious due to its high value of recognition. Both leaf types are also known from the Middle Eocene Geiseltal (Barthel 1976), Messel (Frankenhaeuser & Wilde 1993) and Early Oligocene deposits of Haselbach (Mai & Walther 1978).

**Monocotyledons**

Remains of monocotyledons are rare within the Sulzigtobel flora. Two leaf fragments can be assigned to Smilax sp. (Smilacaceae) (Fig. 5 B-C). Extant species of Smilax are distributed in tropical, subtropical and temperate regions. Fossil members of this genus are known from Oligocene (Kvaček & Walther 1998, 2004; Walther & Kvaček 2007) and Miocene deposits in Europe (Kvaček 1998; Kovar-Eder et al. 2004).

A number of fragmentary strap like leaves, with parallel venation might represent remains of grasses (Poaceae vel Cyperaceae gen. et sp. indet.; Fig. 5 F), but preservation is too poor for more specific identification. A few remains resemble leaves of Typha, an element of the vegetation of shallow water zones. These remains probably represent former parts of the vegetation growing in shallow water and on the banks of the pond, in which the plants were deposited. However, a definite determination of these monocotyledon fossils is not possible at present (Fig. 5 D-E).

**Dicotyledons**

The Sulzigtobel taphoflora is clearly dominated by dicotyledones. The most abundant taxon within the fossil leaf assemblage is Daphnogene polymorpha (A. Braun) Ettingsh. (Fig. 5 G-K; Fig. 6 A-B), a member of the Lauraceae family. The great majority of the variable leaves of this taxon are rather small with dominating lanceolate forms (Fig. 5 G-I). These can probably be interpreted as sun-leaves as in other taxa of Daphnogene (Kvacek & Walther 1974). The cuticle of this taxon is coriaceous on the adaxial side with imprints of regular isodiametric cells. The abaxial side is medium-thick to thin, revealing undulated to slightly waved cell wall structures and numerous trichomes. These surround the slightly sunken, hardly recognizable stomata, which cluster together in groups. Particular structures resemble those of D. cinnamomifolia from the Early Oligocene Fundstätte in Flörshheim, Germany (but see Kvaček 2004).

Other frequent taxa of the Sulzigtobel collection are poplar leaves (Salicaceae) which are assigned to Populus cf. zaddachii Heer (Fig. 61-K) and somewhat enigmatic leaves which are provisionally named Dicotylophyllum sp. A (Fig. 7 A-D).

The earliest fossils of Central European Populus date back to the Early Oligocene, being known from a large number of Miocene floras (Mai 1995). The fossil leaf remains of Sulzigtobel closely resemble leaves of Populus zaddachii Heer, but due to the fact that cuticles show no diagnostic features typical for this species (Fig. 8 E-F), we refrain here from a definite assignment to this species. Adaxial cuticle structures show straight to undulated cell walls and oval to elliptic shaped (paracytic?) stomata. The aperture is spindle shaped and exhibits strongly cutinized outer ledges. Populus zaddachii Heer is mainly known from Oligocene and Early Miocene deposits (e.g. Teodoridis 2003; Reuschel & Walther 2006), but also a few occurrences in Middle Miocene floras are reported (e.g. Plamarev et al. 2005). According to Reuschel & Walther (2006) Populus zaddachii can either be a member of riparian vegetation or mixed mesophytic forests.

The abundant leaves named here Dicotylophyllum sp. A exhibit a venation pattern that is found in Cornaceae. The morphology of these leaves is similar to leaves of the modern genus Dendrothenthomia Hutch, as already observed by O. Appert (O. Appert, pers. comm. 2004). Some authors include this genus within Cornus L. sensu lato (with ca. 60 modern species) representing an East-Asian group with large petaloid floral bracts (Eyde 1987; Xiang & al. 2005). One species of this group, Cornus kousa Bürger ex. Miq., closely resembles the fossil leaf remains of Sulzigtobel in terms of leaf morphology and venation pattern. Fossil leaves and fruits of Cornus were widely distributed in the Northern hemisphere during the Tertiary (Manchester & al. 2009). Mastixia, another genus of Cornaceae, exhibits comparable leaf forms. It is nowadays restricted to warm-temperate regions of Southeast-Asia, but carpologocial remains of this genus are well documented in Tertiary records of the Northern hemisphere (Martinetto 2011; Hably & Erdei 2013). No cuticles could be prepared so far from the Sulzigtobel-leaves, which may have allowed an explicit determination of the genus. Therefore, we assign this morphotype to the fossil-genus Dicotylophyllum.
Fig. 6. Leaves from the Miocene locality Sulzigtobel near Werthenstein (Switzerland): A) Comptonia sp. vel Myrica oehningensis; scale bar = 1 cm; Inv.-Nr. ETHZ 42, 01, 03/15; B) Comptonia sp. vel Myrica oehningensis; scale bar = 1 cm; Inv.-Nr. ST 69-199; C) Myrica cf. lignitum; scale bar = 1 cm; Inv.-Nr. ETHZ 42, 01, 10/4; D) Myrica cf. lignitum; scale bar = 1 cm; Inv.-Nr. ST 69-266; E) Indeterminable leaf fragment with pinnately arranged leaflets; scale bar = 1 cm; Inv.-Nr. ST 69-37; F) Berchemia multinervis; scale bar = 1 cm; Inv.-Nr. ST 69-48; G) Berchemia multinervis; scale bar = 1 cm; Inv.-Nr. ST 69-102; H) cf. Thevetia sophiae; scale bar = 1 cm; Inv.-Nr. ETHZ 42, 01, 02/13; I) Populus cf. zaddachii Heer; scale bar = 1 cm; Inv.-Nr. ETHZ 42, 01, 07/9; J) Populus cf. zaddachii Heer; scale bar = 1 cm; Inv.-Nr. ST 69-58; K) Populus cf. zaddachii Heer; scale bar = 1 cm; Inv.-Nr. ETHZ 42, 01, 02/16.
Fig. 7. Leaves from the Miocene locality Sulzigtobel near Werthenstein (Switzerland): A) *Dicotylophyllum* sp. A; scale bar = 1 cm; Inv.-Nr. ETHZ 42, 01, 04/11; B) *Dicotylophyllum* sp. A; scale bar = 1 cm; Inv.-Nr. ST 69-344; C) *Dicotylophyllum* sp. A; scale bar = 1 cm; Inv.-Nr. ST 69-42; D) *Dicotylophyllum* sp. A; scale bar = 1 cm; Inv.-Nr. ETHZ 42, 01, 08/4; E) *Dicotylophyllum* sp. B; scale bar = 1 cm; Inv.-Nr. ST 69-127; F) cf. *Acer tricuspidatum* Bronn; scale bar = 1 cm; Inv.-Nr. ETHZ 42, 01, 17/3; G) cf. *Salix* sp.; scale bar = 1 cm; Inv.-Nr. ST 69-47; H) cf. *Salix* sp.; scale bar = 1 cm; Inv.-Nr. ST 69-121; I) *Dicotylophyllum* sp. C; scale bar = 1 cm; Inv.-Nr. ST 69-287; J) *Dicotylophyllum* sp. C; scale bar = 1 cm; Inv.-Nr. ETHZ 42, 01, 01/1.
The fossil leaf assemblage of Sulzigtobel comprises a number of taxa with only few (or even single) occurrences. Some of these leaf fragments can be assigned to Comptonia sp. vel Myrica oehningenensis (A. Braun) Heer (Fig. 6 A-B) based on morphological characters, but a more specific determination is not possible based on the fragmentary material.

Two basal leaf fragments can be compared to Myrica lignitum Unger (Fig. 6 C-D), but without knowledge of the characteristic cuticular structures a definite determination is not possible (Walther 1999).

A single fragment of a delicate pinnate leaf (Fig. 6 E) might represent a member of Leguminosae, but due to the fragmentary and overall poor preservation (e.g. entire margins seem toothed in most pinnae due to mechanical damage) an unambiguous affiliation to this or any other group of dicots is not possible.

A few leaves can be determined as Berchemia multinervis (A. Braun) Heer (Rhamnaceae, Fig. 6 F-G) which is also known from a number of other Miocene localities in the NAFB and its surroundings (e.g. Hantke 1954; Mai 1995; Kvaček 1998; Kovar-Eder &
al. 2004; Uhl & al. 2006). Modern species of this genus grew preferably on wet and permeable soils, similar to many species of *Populus*.

Four or five narrow leaves, with obviously coriaceous lamina and revolute margin can be compared to *Thevetia sophiae* (Weber) Palamarev et Petkova (Fig. 6H) an Apocynaceae taxon that has previously been reported from a number of Miocene localities (e.g. Weber 1852; Hantke 1954; Mai 1995).

Some leaves named by us as *Dicotylophyllum* sp. B (Fig. 7 E) show some superficial similarities to the genus *Daphne* L., as their general morphology and venation pattern corresponds to the pattern frequently seen in this genus. However, at the moment a definite determination of these specimens is not possible.

Several leaves can be compared to the genus *Salix* (Salicaceae) without further specific determination (Fig. 7 G-H). *Salix* is also a member of riparian vegetation, growing near the pond or an assumed tributary.

Three fragmentary leaves with a distinct morphology, venation pattern and epidermal pattern cannot be assigned to any specific taxon and are thus treated here as *Dicotylophyllum* sp. C (Fig. 71-J; Fig. 8 C-D). Based on leaf morphology it is not possible to assign these leaves to a certain family. Comparable teeth can be found in a number of *Fagaceae* (e.g. *Castanea, Lithocarpus, Quercus*), but also in some *Betulaceae*, e.g. the modern *Alnus* formosana from Asia. However, leaf margins in *Betulaceae* are often double serrate (e.g. several species of *Betula* and *Alnus*). Abaxial cuticles (Fig. 8C) of this taxon exhibit anomocytic to cyclocytic stomata (apparently with two rings of subsidiary cells). The oval, spindle shaped apertures exhibit slender tips at the poles, the outer ledges of the aperture is strongly cutinized. Adaxial cuticles (Fig. 8 D) are medium thick to thick with regularly arranged, straight walled isodiametric cells and (multicellular) trichome bases. A combination of cuticular anatomy and leaf morphology does also not allow for a unequivocal taxonomic affiliation of these leaves. Anomocytic to cyclocytic stomata and the form of the apertures point to *Fagaceae* (e.g. *Castaneophyllum*, cf. Kvaček & Walther 2010), but similar forms may also occur in *Alnus* and *Betula*, or even *Populus* (cf. Worobiec & Szyrkiewicz 2007; Lin & al. 2010). A comparable epidermal structure has also been described from cuticles from the Miocene flora of Mataschen in Austria, but also in this case a definitive determination was not possible (Kovar-Eder & Hably 2006; Plate 8, Fig. 7 b).

Only a single leaf specimen can be compared to *Acer tricuspidatum* Bronn based on morphological characteristics (Fig. 7 F), which agree well with specimens of this taxon from numerous other localities (e.g. Hantke 1954; Walther 1972). This specimen from the ETH Zurich collection is preserved in a fine and light marl, which is not found in any other specimen from the Sulzigtsobel. It is possible that this specimen represents a special type of sedimentological facies otherwise not sampled by O. Appert. However, it is also possible that this specimen has erroneously been included in the material originating from the Sulzigtsobel. The lithology closely resembles the plant-bearing marls from the locality Schrotzburg near Lake Constance, where *Acer tricuspidatum* is rather common (Hantke 1954; Uhl & al. 2003, 2006), but at the moment it is not possible to exclude the possibility that this specimen comes from a special facies at the Sulzigtsobel.

**Taphonomy, palaeoclima and palaeoenvironment**

All in all it can be concluded that the Sulzigtsobel flora is only moderately diverse in comparison to other Miocene floras from the NAFB (e.g. Schrotzburg: Hantke 1954; Parschlug: Kovar-Eder & al. 2004). We identify 15 different leaf morphotypes, not all of these reliably identified to generic or even specific levels for the time being. One reason for this probably is the limited size of the exposure in the Sulzigtsobel and thus a relatively small number of specimens which were available for this study. Another, more important reason, is the generally very poor and fragmentary preservation of leaves of this locality.

So far no lithological study has dealt with the plant bearing sediments of the Sulzigtsobel in detail. Based on the observations in the field, lithology of hand specimens and the general geological setting, it seems likely that the marls and siltstones were deposited in a pond on the poorly drained alluvial plain environment of the Napf alluvial fan.

Weidmann & Reichel (1979) mentioned relatively small, indeterminate avian footprints from the plant bearing marls at Sulzigtsobel indicating (at least temporary) low water levels for the environment in which the leaves were deposited. As it is not clear from which exact spot of the fossil bearing sediment band the bird tracks originated, it seems possible that such low levels caused oxygenation and bioturbation, which might
have negatively influenced conditions of deposition. According to O. Appert (pers. comm. 2009) the best preserved leaves come from the channel-like structure at the western end of the horizon, where thicker sediments have been deposited. Unfortunately information about the exact finding spots within the plant bearing horizon is missing for the large majority of specimens.

The plants, from which the fossil leaves originate, probably grew directly in the environment of the alluvial fan delta. The landscape on this fan was rather dynamic, due to high rates of water and sediment discharge from the Alps (Kuhlemann & Kempf 2002) leading to constantly shifting channels of braided rivers and areas of sedimentation and erosion. Most taxa occurring in the marls of Sulzigtobel probably originated in the riparian vegetation at the banks of a (hypothetical) watercourse feeding the pond, or directly from the bank of the pond (e.g. Daphnogene polymorpha, Populus cf. zaddachii, cf. Lygodium kaulfussii, Poaceae vel Cyperaceae gen. et. sp. indet., Typha sp., Myrica cf. lignitum, cf. Salix sp., cf. Acer tricuspidatum). Some of these taxa (e.g. Daphnogene polymorpha, Populus cf. zaddachii, cf. Acer tricuspidatum), together with taxa like Berchemia multinervis, and Smilax, could have also been part of some zonal type of forest growing on better drained parts of the Napf alluvial fan. Unfortunately the flora is not diverse enough (in terms of species richness) to allow for an unambiguous reconstruction of certain (?) type(s) of vegetation.

The abundance of leaves assignable to Daphnogene polymorpha and the occurrence of taxa like cf. Thevetia sophiae, Berchemia multinervis and cf. Lygodium kaulfussii points to (warm-)temperate climatic conditions, which is in general accordance with climatic analysis of other macrofloras from the Upper Freshwater Molasse (e.g. Uhl & al. 2003, 2006). However, due to the low species richness of the Sulzigtobel-flora and many taxonomic uncertainties we did not apply any quantitative techniques to this flora so far.

A preliminary palynological analysis of the marls produced a rather low diverse microflora, dominated by wind-transported pollen of Pinus, together with abundant microcharcoal (M. Herrmann, pers. comm. 2010). Pinus-pollen can be transported over great distances by wind and probably represents a component of the vegetation in the hinterland (maybe in the upfolding Alps south of the Napf fan). The occurrence of microcharcoal is also known from other Miocene localities in the German (e.g. locality Hammerschmiede/Germany; Uhl, pers. observation) and Austrian part of the NAFB (e.g. Hausruck lignite/Austria; Masselter & Hofmann 2005). This widespread occurrence of charcoal in the Miocene of the NAFB indicates that paleowildfires were probably a common kind of disturbance during this period. However, so far no macro-charcoal has been discovered at the Sulzigtobel, which could be identified taxonomically, giving us information about the taxa which were affected by fire.

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References


