

A noteworthy plant taphocoenosis from the Lower Oligocene Haselbach Member (Saxony, Germany) containing *Apocynophyllum neriifolium* Heer

LUTZ KUNZMANN and HARALD WALTHER

Natural History State Collections Dresden, Museum of Mineralogy and Geology, 01109 Dresden,
Koenigsbruecker Landstrasse 159, Germany;
e-mail: lutz.kunzmann@snsd.smwk.sachsen.de, h.walther.dresden@t-online.de

Received 28 June 2006; accepted for publication 28. February 2007

ABSTRACT. Mass accumulations of *Apocynophyllum* leaves in a distinct plant taphocoenosis are described from the Lower Oligocene Haselbach Member, Borna Formation of the Weissester Basin (Saxony, Central Germany). These leaves are assigned to the morphospecies *A. neriifolium* Heer 1861 emend. (cf. Lythraceae). Plant taphonomic characters were studied to interpret this taphocoenosis as a parautochthonous assemblage. The assemblage was derived from a *Taxodium* swamp with dense stands of *Apocynophyllum neriifolium*. The plant litter accumulated in a standing water environment.

KEY WORDS: *Apocynophyllum*, floral complex, palaeoecology, plant taphonomy, Oligocene, Haselbach, Weissester Basin, Germany

INTRODUCTION

The Tertiary of Central Europe have been investigated palaeobotanically, palynologically, and geologically for more than 150 years. Detailed climate-stratigraphic subdivision of the Tertiary in the Boreal province of Central Europe is based on these floras, and the interpretations are widely accepted today. These subdivisions utilize both megafloral assemblages (“Florenkomplexe”, Mai & Walther 1983) and palynofloras (spore-pollen-zones, Krutzsch 1967), because each provides a different perspective on the local and regional flora (Gastaldo et al. 1998).

The period of discovery and description of numerous rich floras within the Weissester Basin ended with the closure of most of the open cast mines in this area of Central Europe (e.g. Engelhardt 1870, Mai & Walther 1978, 1985, 1991). Presently, taphonomic, palaeoecologic, and palaeosociologic investigations of some of the well known localities have become

the focus of study (Gastaldo et al. 1996, 1998, Walther & Kunzmann in prep.). But, due to abundance of fossil material still available for study, new taxa have been identified that supplement the floral lists of these localities (Kunzmann 1997).

The Haselbach Clay of the Haselbach Member (lowermost Oligocene) – one of the horizons rich in fossil plants – currently is exposed in the open cast mine “Vereinigtes Schleenhain” of the MIBRAG mbH near Borna in Saxony, Germany. Floras preserved within the Haselbach Member provide evidence for a major turnover in vegetation in response to climate in the European Palaeogene (Kvaček & Walther 2001). The details of this turnover in space and time that occurred close to the Eocene/Oligocene boundary in Central Germany is not well described, and it seems that the turnover may have been a sudden event over the course of a few 10 000 years. A multi-

disciplinary research group was established to investigate timing and rate of turnover in the flora. A preliminary result of this research project is the discovery in 2005 of a noteworthy plant taphocoenosis from the Lower Oligocene Haselbach Member. Details of this assemblage are presented herein.

THE HASELBACH ASSEMBLAGE

Paleoecological and climatic changes in the European Oligocene are recognized in the Boreal province of Central Europe by the presence of rich megaflores from lowland coastal plains and volcanoclastic deposits in hinterlands (volcanic floras sensu Kvaček & Walther 1998). Many of these floras have been evaluated critically and compared using a suite of revised or emended megafloral assemblages or “Florenkomplexe” (Kvaček & Walther 2001). Seven floral assemblages have been recognized in the (Atlantic-) Boreal province of Central Europe (Mai 1995) depending on periodic introduction of “modern” arcto-tertiary elements in response to palaeoclimatic and palaeogeographic changes (Kvaček 1994, Walther 1994). The major vegetational turnover occurred in the earliest Lower Oligocene with the appearance of taxa in the latest Upper Eocene. The Haselbach floral assemblage (Mai & Walther 1978, Kvaček & Walther 2001) is characterized by new intrazonal vegetation units that include aquatic *Salvina* associations, *Nyssa-Taxodium* swamp forest, and riparian forests containing deciduous broad-leaved elements like *Salix*, *Populus*, *Alnus*, *Ulmus*, *Carpinus*, and *Acer*, which continue to develop in the Neogene. The zonal vegetation is recognized by the introduction of elements of a Mixed Mesophytic Forest, both by carpological taxa (e.g. *Carya*, *Engelhardia*, *Eomastixia*, *Eurya*, *Manglietia*, and *Mastixicarpum*) and leaf taxa of the genera *Engelhardia*, *Myrica*, *Pyracantha*, *Rosa*, *Eotriponobalanus*, and *Tetraclinis*. Walther (1990) reconstructed a variety of forest types and plant associations of the Haselbach assemblage based on these assemblages.

MATERIAL AND METHODS

The fossil plant material was collected from the Haselbach Member of the Weissester Basin. The Weissester Basin is the southern part of the Leipzig

Basin and contains middle Eocene to early Miocene terrestrial, brackish, and also marine sedimentary sequences. The Haselbach Member is assigned to the lowermost part of the Borna Formation C, and is considered to be probably lowermost Oligocene in age based on palynological and palaeobotanical data (Krutzschn 1967, Mai & Walther 1978, 1983, Krutzschn et al. 1992, Mai 1995, Eissmann 1994, 2004, 2005, Deutsche Stratigrafische Kommission 2002, Rascher et al. 2005). The Borna Formation C consists of fluvial, estuarine, marginal marine deposits and the terrestrial lignite complex “Böhlen” (bed IV of the Weissester Basin). For a more detailed stratigraphical and geological description see Eissmann (2004), Deutsche Stratigrafische Kommission (2002) and Rascher et al. (2005).

The Haselbach Member mainly consists of the Haselbach Clay (clay as a technological term), which is the sedimentary expression of a relatively stable system consisting of larger anastomosing and smaller meandering rivers running through a heterogeneous floodplain (Kunzmann & Walther 1997). Abandoned channel, levee sediments, crevasse splay deposits, and floodplain mud are common facies in the Haselbach Clay. In Schleenhain, the Haselbach Clay is divided into a lower and an upper unit. The material reported herein was part of an abandoned channel or oxbow lake deposit within the lower Haselbach Clay. Such deposits are famous for their rich parautochthonous and partly autochthonous megafloral assemblages (Kunzmann 1995), which originated from several plant communities. The taphocoenosis of the Haselbach Clay in Schleenhain represents mainly riparian forests, a *Taxodium* backswamp and elements of a mesophytic forest (Mixed Mesophytic Forest, Mai & Walther 1978, Kunzmann & Walther 1997). Fining upward sedimentary sequences characterize abandoned channels or smaller temporary lake floodplain deposits. There are generally planar laminated, fine grained sand and/or silt alternating with silty clay and phytoclasts.

The material used in this study consists of a single sediment block of a lake or abandoned channel deposit from the open cast mine “Vereinigtes Schleenhain” of the MIBRAG mbH near Borna, Borna County, Saxony, Germany (2nd working level, 27.05.2005). The plant remains (leaves, short shoots, cone scales, fragments of branches, woody debris) are exposed mainly on a single bedding surface of this block, which is ~800 mm long, ~380 mm wide (~800 cm² surface area). Some remains are from other bedding planes of the block, which are cut at the block’s margin. At least 167 remains were observed (Fig. 1; Pl. 1, fig. 1).

The fossil plants are preserved as impressions and/or coalifications with cuticles preserved. Small fragments of leaf cuticles were removed from specimens and macerated for 1–4 minutes in Schultze solution. Cuticles then were neutralized with NH₄OH and washed with distilled water. The cuticles were stained with safranin, affixed to slides for LM studies, and studied using a Leica Aristoplan Microscope. The fossils were studied using a Leica MZ APO Microscope equipped with a camera lucida, and a digital DFC 320 camera. Some photographs were taken with a Nikon D200 digital camera equipped with a 60 mm Nikkor macro-objective.

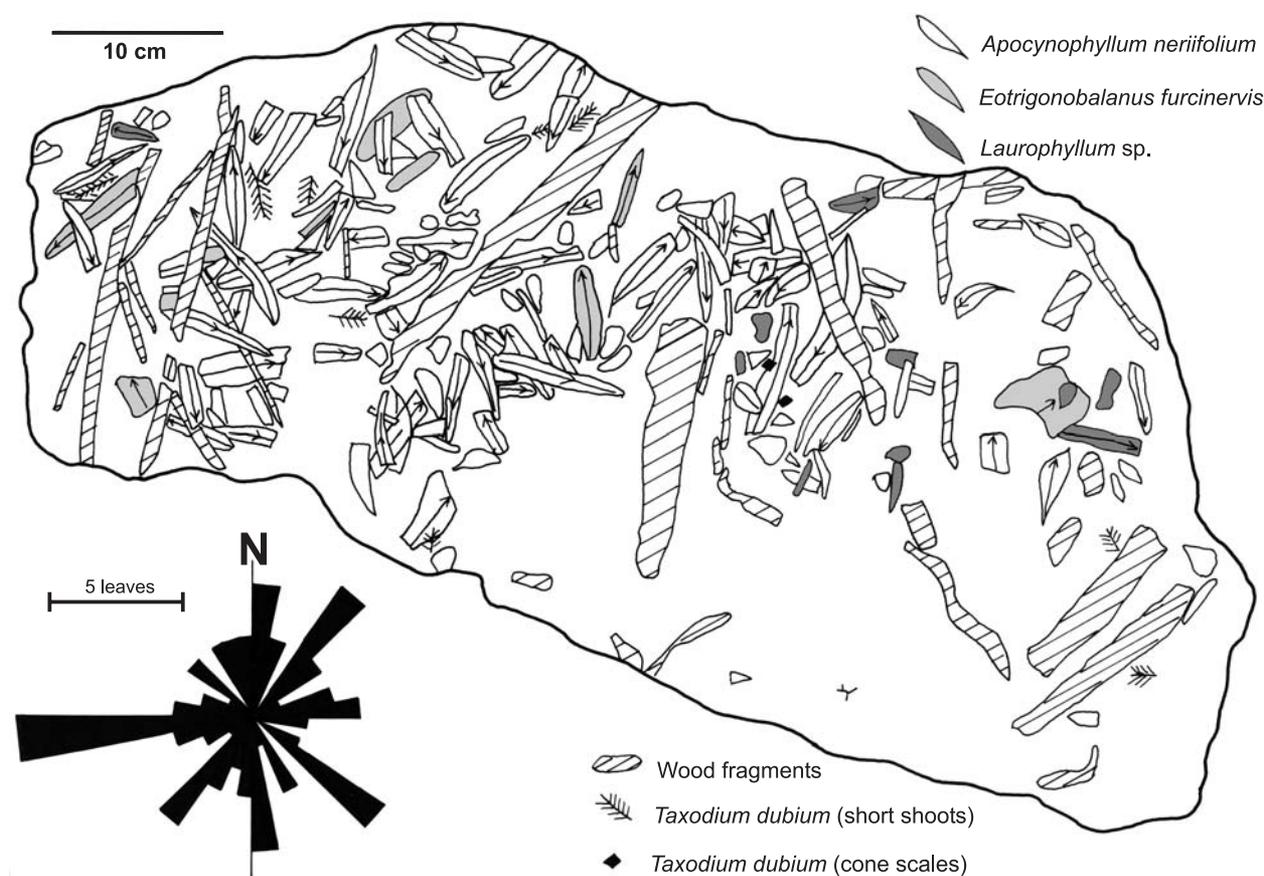


Fig. 1. Line drawing of bedding surface of sediment block of the open cast mine “Vereinigtes Schleenhain” showing distribution of taxa; planar orientations of leaves are outlined by arrows on the midvein; rose diagram showing planar orientation (relative to arbitrary north) of 90 angiosperm leaves, leaf fragments and *Taxodium* shoots from the bedding surface (*Apocynophyllum neriifolium* – 63, *Taxodium dubium* – 10, *Eotrigonobalanus furcinervis* – 8, Dicotyledonae gen. et spec. indet. – 9). MMG Schle MO 556

All material is housed at the Palaeobotanical Collection of the Museum of Mineralogy and Geology of the Natural History State Collections Dresden (MMG PB Schle MO 556). The taxonomy and systematics used in this study follow Takhtajan (1996).

The following phytotaphonomic data were recorded: (1) planar orientation of individual leaves and conifer short shoots, and (2) orientation of leaf surfaces. Planar orientations were made in the direction of the leaf apex or towards the apex of short shoots. Data were organized into 32 intervals of 11.25° ($= 360^\circ$) and plotted as a rose diagram. The disposition of individual leaves relative to adaxial or abaxial side up was determined using venation patterns. The exposed surface was considered to be abaxial if venation was in surficial relief.

SYSTEMATIC DESCRIPTION

Of all taxa identified, only *Apocynophyllum neriifolium* Heer emend. will be described and discussed comprehensively. Detailed descriptions of other morphospecies found in the present investigation do not contribute substantially to the present knowledge of these

taxa. Table 1 provides an overview of all identified taxa and their frequency of occurrence within the sample block.

cf. *Lythraceae* Jaune Saint-Hilaire

The Lythraceae are a rather heterobathmic family. Primitive characters, such as superior ovary and monosporic female gametophyte of the *Polygonium*-type, are combined with advanced characters, such as pinnate venation of the petals and the dominance of herbs (Takhtajan 1996). The family is subcosmopolitan, but mainly distributed in tropical and subtropical regions, especially in America. There are relatively few species (mostly annual or perennial herbs) that presently occur in temperate and cold areas.

Morphogenus *Apocynophyllum* Unger 1850

This morphogenus is circumscribed for simple, entire margined, lanceolate leaves with a strong midvein and dense brochidromous secondary veins that are joined

Table 1. List of macrofossil plant remains from sediment block Schle MO 556 collected in the open cast mine “Vereinigtes Schleenhain” near Borna, Saxony, Germany, Haselbach Member, Borna Formation, lowermost Lower Oligocene

Species/phytocolast	Number of specimens	Collection numbers	Cuticle preparation slides
<i>Taxodium dubium</i> (Sternberg 1823) Heer 1855 (Cupressaceae)	11 short shoots 2 cone scales	MMG PB Schle MO 556: 1, 8, 33, 34, 50, 63, 64, 71, 134, 163, 166 MMG PB Schle MO 556: 123, 124	Schle MO 01/05-07/05 of shoot 556: 1
<i>Eotrigonobalanus furcinervis</i> (Rossmässler 1840) Walther & Kvaček in Kvaček & Walther 1989 forma <i>haselbachensis</i> (Fagaceae)	10 leaves and leaf fragments	MMG PB Schle MO 556: 2, 3, 6, 13, 27, 42, 47, 95, 103, 155	Schle MO 08/05-11/05 of leaf 556: 2, Schle MO 12/05 of leaf 556: 3
<i>Apocynophyllum neriifolium</i> Heer 1861 emend. (cf. Lythraceae)	110 leaves and leaf fragments	MMG PB Schle MO 556: 4, 5, 9, 14, 15, 16, 17, 18, 19, 21, 22, 23, 24, 25, 26,, 28, 29, 30, 31, 32, 35, 36, 37, 38, 39, 40, 41, 43, 44, 45, 46, 48, 49, 51, 53, 54, 55, 56, 57, 58, 59, 60, 61, 62, 65, 66, 67, 68, 70, 72, 74, 75, 76, 77, 79, 80, 81, 82, 83, 84, 85, 86, 88, 89, 90, 91, 92, 93, 94, 96, 98, 99, 100, 101, 102, 107, 108, 109, 110, 111, 112, 113, 114, 115, 116, 117, 118, 119, 121, 125, 126, 129, 131, 132, 133, 138, 140, 142, 144, 145, 146, 147, 150, 151, 153, 155, 160, 165	Schle MO 13/05-17/05 of leaf 556: 4
<i>Laurophyllum</i> sp. (Lauraceae)	11 leaves and leaf fragments	MMG PB Schle MO 556: 10, 120, 127, 130, 135, 136, 141, 148, 154, 158, 159	–
Dicotyledonae gen. et spec. indet.	34 leaf fragments	MMG PB Schle MO 556: 11, 12, 20, 52, 73, 78, 87, 97, 104, 105, 106, 120, 122, 127, 128, 130, 135, 136, 137, 139, 141, 143, 148, 149, 152, 154, 156, 157, 158, 159, 161, 162, 164, 167	–
Wood fragments	23	–	–

into an intramarginal vein. The genus was erected by Unger (1850) for leaves from the middle Miocene locality of Radoboj in Croatia. Within the genus are 3 closely related species. Originally the genus name was chosen to suggest leaf characters that were similar to leaves of the extant *Nerium oleander* Linné (Apocynaceae). Today, any attempts at understanding the phylogenetic relationships of the taxon using the name, alone, could be misinterpreted. Subsequently, some authors used *Apocynophyllum* to erect new species for fossil leaves that might be representatives of the Apocynaceae based on their macro-morphology (Heer 1859). Kräusel and Weyland (1950) noted that there were similar cuticle characters between *Apocynophyllum helveticum* and extant Apocynaceae. More recently, *Apocynophyllum* was in use as a leaf morphogenus of unknown family affinity (e.g. Mai & Walther 1991). But, this morphogenus is validly published according to the ICBN (Greuter 2000) and the name must be retained.

The family and generic affinities have been

problematic for a long time due to the lack of known reproductive structures. Kvaček and Sakala (1999) reported on a leafy twig with fruits of *Decodon gibbosus* (E. M. Reid) Nikitin 1929 that were assigned to the Lythraceae. These originated from the Lower Miocene of Bilina, Most Basin, North Bohemia, Czech Republic. The attached leaves correspond in their features to *Apocynophyllum helveticum* Heer and “*Ficus*” *multinervis* Heer. Kvaček and Sakala (1999) also discussed the possible affinity of other *Apocynophyllum* species and related species like “*Ficus*” *multinervis* Heer 1856 to the Lythraceae, but there is no empirical evidence, to date, in the fossil record.

Lanceolate leaves with dense secondary venation and an intramarginal vein occur also in other angiosperm genera and families; for example, Moraceae (*Ficus*), Apocynaceae (*Periploca*), and Myrtaceae. Assignment of a morphology to a genus is impossible on the basis of macromorphology and venation pattern, alone. Hence, *Apocynophyllum* Unger is used in the present studies as a morphogenus

for isolated leaves that show morphological and anatomical affinities to the leaves of the family Lythraceae.

Apocynophyllum neriifolium Heer 1861
emend.

Fig. 2; Pl. 1–3

- 1861 *Apocynophyllum neriifolium* Heer, p. 419, pl. 6, figs 12 f–g, pl. 8, figs 1–8. (type material)
1869 *Apocynophyllum attenuatum* Heer; Heer, p. 37, pl. 9, figs 7–9.
1869 *Apocynophyllum elongatum* Heer; Heer, p. 38, pl. 8, figs 10–15, pl. 9, fig. 5b, pl. 26, figs 15–16.
1950 *Apocynophyllum helveticum* Heer; Kräusel & Weyland, p. 75, pl. 19, figs 3–7, Textfigs 31, 32.
1976 *Apocynophyllum neriifolium* Heer; Rufflé et al., p. 269, pl. 39, figs 6–9.
1978 *Apocynophyllum helveticum* Heer; Mai & Walther, p. 128, pl. 4, figs 1–5, pl. 46, figs 7–13, pl. 47, figs 1–3.

For more synonyms see Kräusel & Weyland (1950) and Mai & Walther (1978).

Emended diagnosis. Leaves simple, petiolate, entire margined, oblong-lanceolate to oblong-ovate in shape, apex acuminate, base cuneate. Venation brochidodromous with prominent intramarginal vein, four or more secondary veins per cm of the midvein length, one to three intersecondary veins between two secondaries. Cuticles slightly to distinctly wrinkled or partly finely striate, stomata anomocytic, occasional paracytic, simple trichome bases scattered on both side.

Type material: *Apocynophyllum neriifolium* Heer 1861, p. 419, pl. 6, figs 12 f–g, pl. 8, figs 1–8 from Schkopau near Halle (“Knollensteine”), Sachsen-Anhalt, Germany, Upper Eocene.

Material from Schleenhain: 110 leaves and leaf fragments (Table 1), cuticle preparation slides Schle MO 13/05-17/05 of leaf MMG PB Schle MO 556 : 4.

Description. Detached simple petiolate leaves of delicate consistence that are oblong-lanceolate to oblong-ovate in shape and entire margined. The widest part is within the lower third of the lamina. The leaf laminae often are slightly to distinctly curved along their long axes, but are not or very slightly asymmetrical with respect to the width of the lamina on opposite sides of the primary vein (Pl. 2,

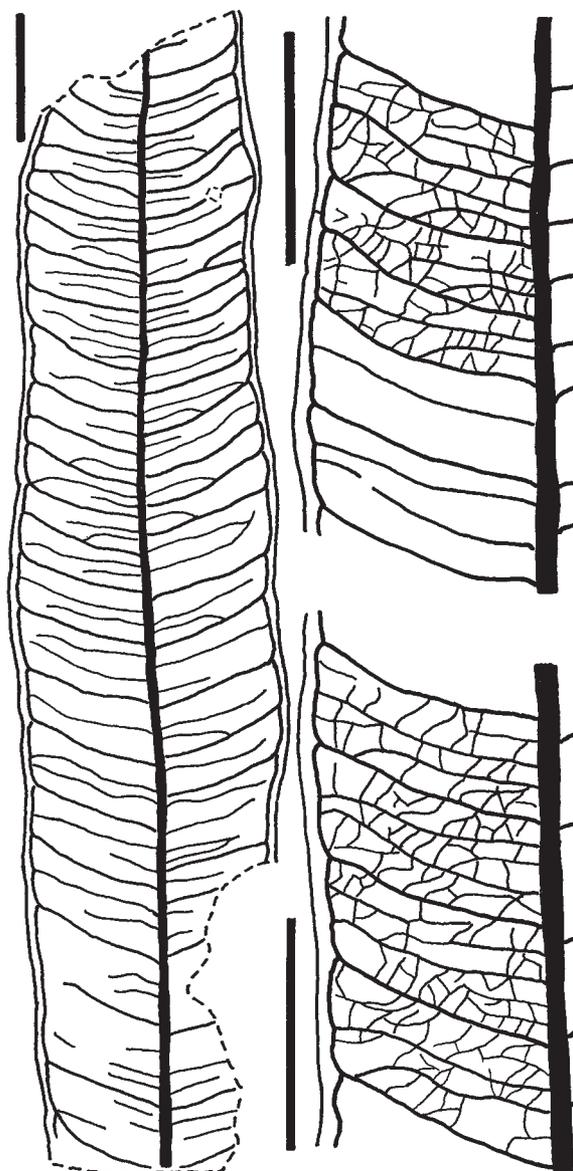


Fig. 2. Venation pattern of *Apocynophyllum neriifolium* Heer 1861 emend., leaf fragment and two details, open cast mine “Vereinigtes Schleenhain” near Borna, Saxony, Germany, Haselbach member, Borna Formation, lowermost Lower Oligocene, MMG Schle MO 556 : 93, camera lucida drawing, scale bar – 5 mm

fig. 1). The distal leaf gradually tapers into an acuminate apex; the proximal leaf gradually develops into a cuneate leaf base with a short peduncle (Pl. 2, fig. 3). In the present study, no leaf is preserved completely. The largest leaves are >100 mm in length (Schle MO 556 : 140) whereas the width of the leaves ranges from 7–28 mm. The petiole is at least 7–9 mm long.

The leaf venation is characterized by dense brochidodromous secondary veins joined into an intramarginal vein (Fig. 2; Pl. 2, figs 5–7). The primary vein is prominent on both sides of the lamina, while higher-order venation

is very thin and clearly visible only on the abaxial side. Only some of the secondary and intersecondary veins could be observed also on the adaxial side. Secondary veins spread in an opposite to subopposite pattern with angles that range from 50–86° from the midvein. The trend straight or slightly curved (convex, concave or s-shaped) to the intramarginal vein, which is about 0.5 mm from the margin. There is an average of 4–9 secondary veins per cm of margin length. Often, there are 1–3 intersecondary veins inbetween two secondaries, which usually run from the midvein to the intramarginal vein or to the secondary vein below (Pl. 2, fig. 6). In some cases, the intersecondary veins do not reach the intramarginal vein. The angles of divergence of intersecondary veins spread are similar to those reported above. Secondary and intersecondary veins are interconnected by tertiary and 4° veins, which form a polygonal network. Thin veins that connect the intramarginal vein with the leaf margin are not visible often (Fig. 2).

Cuticles are very thin and delicate. Fungal hyphae often are visible on the cuticles (Pl. 3, fig. 8). The adaxial surface is poorly known. Here, epidermal cells are polygonal and isodiametric in shape with straight or slightly curved anticlinal walls. Cuticle surfaces are slightly to distinctly wrinkled and striated. Abaxial surfaces show ordinary epidermal cells, polygonal and isodiametric in shape, with thin, straight, slightly curved and sinuous anticlinal walls (Pl. 3, fig. 1). Isolated, ring-shaped and moderately cutinized cells are interpreted as trichome bases which are ~16 µm in diameter. The stomata are anomocytic, occasional paracytic, and are elliptical to almost circular in shape. Stomata are scattered over the abaxial surface (Pl. 3, figs 1, 7). Stomata have slightly thickened ledges on both sides of a spindle-like stomatal pit. Anomocytic stomata are 12–20 µm long and 12–16 µm wide.

Discussion. Formerly linear-lanceolate, entire margined leaves with a dense brochidromous venation and an intramarginal vein were identified within the Haselbach complex as *Apocynophyllum helveticum* Heer 1859 (Kräusel & Weyland 1950, Mai & Walther 1978). The type specimen of this morphospecies originates from the late Oligocene to early Miocene of Walkringen near Bern,

Switzerland (Heer 1859, p. 191, pl. 154, figs 2, 3). It lacks cuticular characters. *Apocynophyllum helveticum* differs only slightly from "*Ficus*" *multinervis* Heer 1856 from the Lower Miocene Molasse beds of Switzerland and both taxa are probably conspecific (Kvaček & Sakala 1999). But, synonymy of these taxa is impossible because the type materials lack cuticular structures in both cases.

The new material described herein corresponds with *Apocynophyllum helveticum* recorded from Regis (Kräusel & Weyland 1950) and Haselbach (Mai & Walther 1978), both localities within the Haselbach complex. Previous authors have described several characters that differ from observations made in the present study. For example, Kräusel and Weyland (1950) described two wide lateral subsidiary cells that accompanied paracytic stomata in the taxon. Whereas, Mai and Walther (1978) reported the occurrence of mainly paracytic stomata, while stomata with two lateral and two polar subsidiary cells rarely occurred. The present reinvestigation shows that these purported subsidiary cells were misinterpreted because the anticlinal walls are mostly covered by wrinkles. The "polar and lateral" cells should better be interpreted as ordinary epidermal cells (Pl. 3, figs 3–5).

Kvaček and Sakala (1999) published one twig with fruits of *Decodon gibbosus* (Lythraceae) and attached leaves of cf. *Apocynophyllum helveticum* (without cuticles) from the Lower Miocene of Bílina. They noted that Miocene material from the Most Basin previously published under *A. helveticum* could be assigned to *Decodon* of the Lythraceae. These leaves are characterized by a verticillate phyllotaxy, finely striate and hairless cuticles, and anomocytic stomata on both sides of the lamina. If the leaves from Bílina can be assigned definitely to *A. helveticum*, the material from the Haselbach complex differs in several features as reported by Kvaček and Sakala (1999).

Since the studies of Kräusel and Weyland (1950), *Apocynophyllum neriifolium* was considered as conspecific with *Apocynophyllum helveticum*. Initially, Kvaček and Sakala (1999) reported that the Haselbach material was similar to *Apocynophyllum neriifolium*. This morphospecies originally was erected by Heer (1861) for Upper Eocene impressions from the "Knollensteine" of Schkopau

near Halle, Sachsen-Anhalt, Germany. Heer (1861) stated that *A. neriifolium* is similar to *A. helveticum* but differs in having longer petioles, narrower laminae, thicker midveins, and “slightly” denser secondary venation. The lack of cuticle makes it impossible to acquire additional characters that would allow for a decision on whether these taxa are conspecific.

Rüffle et al. (1976) used the epithet *neriifolium* for material with cuticles preserved from the Upper Eocene of Kayna-Süd, Geiseltal, Sachsen-Anhalt, Germany. They reevaluated the morphospecies and pointed out differences with Middle Eocene leaves they determined as *Apocynophyllum helveticum* from Neumark-Süd, Geiseltal. *Apocynophyllum neriifolium* sensu Rüffle et al. (1976) differs slightly from *A. helveticum* in having narrower leaf blades and denser secondary venation which departs from the midvein at angles less than 30°. The cuticle is without striae. The Geiseltal material shows “Gummikörper,” which are doubtful structures. Although Rüffle et al. (1976) described additional cuticle characters for this morphospecies, they did not emend the diagnosis.

The material from the Haselbach complex (Haselbach, Regis, Schleenhain) is similar in macromorphology to the type of *A. neriifolium*, but differs in having a wider range of leaf-blade width (Pl. 2, fig. 1). *Apocynophyllum neriifolium* from Kayna-Süd (Rüffle et al. 1976) differs by the presence of angles between midvein and secondaries less than 30°. Secondary veins of leaves from the Haselbach complex depart the midvein with angles that range from 50–86° (this study) and 59–80° (Mai & Walther 1978). Cuticular characters of the Haselbach complex material correspond to fossils from Kayna-Süd; these include cuticles that are not or partly striate, and stomata that sometimes are paracytic. Apart from the morphological differences, it is assumed that the Upper Eocene and Lower Oligocene material of the Weissenster Basin belong to the same species, which is distinct from late Oligocene/early Miocene material assigned to *A. helveticum*.

Apocynophyllum neriifolium is distinguished from *A. helveticum* by the presence of denser secondary veins, one to three orders of intersecondary veins, and cuticle characters. *Apocynophyllum helveticum* has almost exclusively finely striate cuticles and is probably

hairless. Due to preservational conditions, though, it is not possible to know if *A. neriifolium* is also amphistomatic like *A. helveticum* (Kvaček & Sakala 1999). Among more than 150 leaves from the Haselbach locality, not one specimen has stomata on the adaxial side (Mai & Walther 1978). Nothing is known about the phyllotaxy of *A. neriifolium*. *Decodon gibbosus* / *Apocynophyllum helveticum* from Bílina is characterized by verticillate phyllotaxy, while extant *Decodon verticillatus* shows decussate and whorled phyllotaxy (Krüssmann 1983).

However, *Apocynophyllum neriifolium* is quite similar to *A. helveticum* and, therefore, the character suite matches the Lythraceae. Kvaček and Sakala (1999) stated that leaves of *A. neriifolium* occur regularly associated with seeds of the extinct Lythraceae *Microdiptera parva* Chandler 1957 and may represent its foliage. *Microdiptera parva* occurs within the Lower Oligocene floras of Schleenhain and Haselbach, but *Decodon gibbosus* also is known from the Haselbach complex (locality Peres; Mai & Walther 1978). In the Upper Eocene locality Kayna-Süd, *Apocynophyllum neriifolium* is associated both with *Microdiptera parva* and with *Decodon gibbosus* (Mai & Walther 1985). Therefore, it is not possible to prove that *Apocynophyllum neriifolium* leaves and *Microdiptera parva* seeds originate from one species.

TAPHONOMY AND PALAEOECOLOGY

Until the present discovery, mass accumulations of *Apocynophyllum* leaves were unknown within the Haselbach complex (Mai & Walther 1978). It appears that the plant remains represent a parautochthonous or nearly autochthonous assemblage. Behrensmeier and Hook (1992) consider an assemblage as parautochthonous if the phytoclasts have been transported away from the death or discard site but have remained within the original habit. Based on the sedimentological data, an allochthonous accumulation concentrated by river or wind transport, or a single “catastrophic” event are considered not feasible to explain the origin of the Schleenhain assemblage.

To verify whether the leaf assemblage could be interpreted as parautochthonous or not, phytotaphonomic criteria of Gastaldo et al. (1996, 1998) were used. These criteria

include: directional orientation of leaves and taxodiaceous branchlets, leaf-surface orientation (adaxial/abaxial), and a log-normal distribution of leaf sizes (ratio length/width) in the assemblage and in the dominant taxa. The last criterion could not be recorded because all *Apocynophyllum* leaves are incompletely preserved. A rose diagram plot of 90 leaves/leaf fragments/*Taxodium* branchlets (Fig. 1) shows a random planar orientation of these phytoclasts on the bedding surface relative to arbitrary north. The orientation of adaxial and abaxial leaf surfaces exposed on the bedding plane also seems to be random. This criterion was evaluated based on 92 of 110 *Apocynophyllum* leaves (55 adaxial side up : 37 abaxial side up) and 7 of 10 *Eotrigonobalanus* leaves (4 adaxial side up : 3 abaxial side up). Both results support the interpretation of parautochthony. Additionally, Kunzmann (1995) considered phytoclast assemblages within two abandoned channel deposits of the Haselbach Member in the Schleenhain opencast mine as parautochthonous.

Based on its similarity to foliage of *Decodon gibbosus* (Kvaček & Sakala 1999), *Apocynophyllum neriifolium* must have had a similar autecology to the extant taxon *Decodon verticillata*. Today, *Decodon* is a monotypic relict genus in North America. It is a deciduous suffruticose aquatic subshrub that forms dense stands in shallow and still waters, in freshwater marshes, along wet shorelines, and within swamp forest clearings. As its common English name "swamp loosestrife" indicates, *D. verticillata* occurs in riparian forests and in *Taxodium-Nyssa* swamps.

The leaf taphocoenosis from Schleenhain contains short shoots and cone scales of *Taxodium dubium* and leaves of *Eotrigonobalanus furcinervis* forma *haselbachensis* and *Laurophyllum* sp. in addition to *Apocynophyllum neriifolium*. A parautochthonous assemblage would indicate that the leaf assemblage directly represents contribution from the plant community in the immediate vicinity of the depositional site. This plant community corresponds to the "*Athrotaxis couttsiae* swamp forest" that was reconstructed by Walther (1990) for an association of the Lower Oligocene Haselbach complex. This association is characterized by large taxodiaceous conifers (e.g., *Taxodium dubium*, *Quasisequoia couttsiae*), *Eotrigonobalanus*, Lauraceae (*Laurophyllum*,

Daphnogene), palmettos (*Sabal*), and ferns. Thus, the fossil assemblages can be compared with extant *Taxodium* swamps containing submersed plant communities with *Decodon verticillata*.

Other mass accumulations of Lythraceae leaves are known from the fossil record (e.g. Pellendorf, Austria, Upper Miocene, Kovar-Eder et al. 2002). Kovar-Eder et al. (2002) describe a mass-occurrence of *Decodon* leaves from the lower part of a hydrophyte pelite, which documents extended, probably monospecific stands of the fossil water willow. The upper part of the pelite preserves a diverse aquatic assemblage along with a few azonal woody taxa that document a facies shift to shallow open water and a nearby riparian or swamp forest. Based on the Pellendorf assemblage, a coastal freshwater marsh with ponds and lakes was reconstructed (Kovar-Eder et al. 2002). For other localities where Lythraceae are reported, see Kvaček and Sakala (1999).

CONCLUSIONS

Apocynophyllum leaves from the Lower Oligocene Haselbach Member, Borna Formation, Weisselster Basin (Central Germany), are assigned to the species *A. neriifolium*, which is distinguished by a combination of morphological and anatomical features from *A. helveticum*. These characters show that *A. neriifolium* is very probably assignable to the Lythraceae. It is not demonstrated, though, that *A. neriifolium* represents the foliage of the morphogenus *Microdiptera*, an extinct Lythraceae.

Apocynophyllum neriifolium from the Lower Oligocene of Schleenhain matches palaeosociological and palaeoecological features of the extant taxon, *Decodon verticillata*, assigned to the Lythraceae. This is demonstrated using taphonomic features of an assemblage in which more than 100 leaves of this morphospecies are preserved on a single bedding plane. Accordingly, *Apocynophyllum neriifolium* is interpreted to have formed dense stands in shallow standing water. Members of the leaf assemblage, in the whole, grew in swamp forest ("*Athrotaxis couttsiae* swamp forest" sensu Walther 1990) with large taxodiaceous conifers (i.e. *Taxodium*), *Eotrigonobalanus*, Lauraceae, palms, and ferns (Fig. 3).

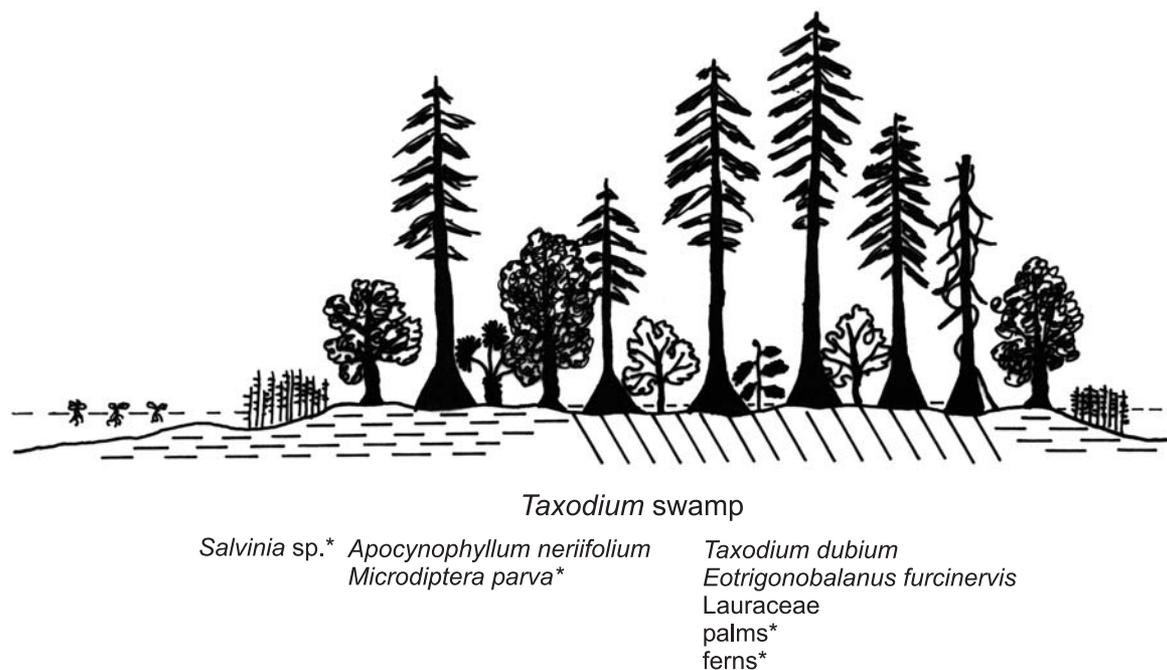


Fig. 3. Reconstruction of an early Oligocene landscape on the basis of fossil plant remains identified on the bedding surface of sediment block MMG Schle MO 556 (after Walther 1990). Floodplain is depicted with *Taxodium* swamp forest and aquatic plants in still waters (small lakes or clearings); taxa with an asterisk occur in this plant community within the Haselbach Member (Mai & Walther 1978) that are not recorded in the present study

ACKNOWLEDGEMENTS

The authors would like to thank Mibrag mbH Theißen, Sachsen-Anhalt (especially to Dipl.-Geol. Thomas Fischkandl) for technical support and permission to collect fossil plant material in the open cast mine “Vereinigtes Schleenhain”.

We also would like to thank Carola Kunzmann (MMG Dresden) who prepared the cuticle slides of the fossil material for the present study. The Botanical Garden of the Technical University of Dresden helped with living material of Lythraceae. We are also thankful to two unknown reviewers for their critical comments and to Dr. Robert A. Gastaldo (Colby College, Waterville, ME, USA), who read the English version of the text critically.

REFERENCES

- BEHRENSMEYER A.K. & HOOK R.W. 1992. Palaeoenvironmental contexts and taphonomic modes in the terrestrial fossil record: 15–136. In: Behrensmeier A.K., Damuth J.D., Dimichele W.A., Potts R., Sues H.-D. & Wings S.L. (eds) *Terrestrial ecosystems through time*. University Chicago Press, Chicago, IL.
- CHANDLER M.E.J. 1957. The Oligocene flora of Bovey Tracey lake basin, Devonshire. *Bull. Brit. Mus. Nat. Hist. Geol.*, 3(3): 1–123.
- DEUTSCHE STRATIGRAFISCHE KOMMISSION (ed.) 2002. *Stratigrafische Tabelle von Deutschland 2002*.
- EISSMANN L. 1994. Leitfaden der Geologie des Präquartärs im Saale-Elbe-Gebiet. In: Eissmann L. & Litt T. (eds) *Das Quartär Mitteldeutschlands. Ein Leitfaden und Exkursionsführer. Mit einer Übersicht über das Präquartär des Saale-Elbe-Gebietes*. *Altenbg. Nat. Wiss. Forsch.*, 7: 11–53.
- EISSMANN L. 2004. Die Braunkohlenformation des Weißelster-Beckens mit einem Abriss des Prätertiärs und Quartärs: 21–39. In: Berkner A. (ed.) *Bergbau in Sachsen, Band 11: Der Braunkohlenbergbau im Südraum Leipzig*. Sächs. Landesamt f. Umwelt u. Geologie, Freiberg/Sachsen.
- EISSMANN L. 2005. Graphische Kompilationen zum Tertiär Mitteldeutschlands (Paralipomena I). *Mauritiana (Altenburg)*, 19(2): 283–288.
- ENGELHARDT H. 1870. *Die Flora der Braunkohlenformation im Königreich Sachsen*. S. Hirzel, Leipzig.
- GASTALDO R.A., FERGUSON D.K., WALTHER H. & RABOLD J.M. 1996. Criteria to distinguish parautochthonous leaves in Tertiary alluvial channel-fills. *Rev. Palaeobot. Palynol.*, 91: 1–21.
- GASTALDO R.A., RIEGEL W., PÜTTMANN W., LINNEMANN U.G. & ZETTER R.M. 1998. A multidisciplinary approach to reconstruct Late Oligocene vegetation in central Europe. *Rev. Palaeobot. Palynol.*, 101: 71–94.
- GREUTER W. 2000 (ed.). *International Code of Botanical Nomenclature*. Koeltz Scientific Books, Königstein.
- HEER O. 1855. *Flora Tertiaria Helvetiae*, vol. 1. Wuster, Winterthur.

- HEER O. 1856. Flora Tertiaria Helvetiae, vol. 2. Wuster, Winterthur.
- HEER O. 1859. Flora Tertiaria Helvetiae, vol. 3. Wuster, Winterthur.
- HEER O. 1861. Beiträge zur näheren Kenntnis der sächsisch-thüringischen Braunkohlenformation. Abh. Naturw. Ver. Prov. Sachs. Thür.: 405–438.
- HEER O. 1869. Miocene baltische Flora. Beitr. z. Naturkunde Preussens, 2: 1–104.
- KOVAR-EDER J., SCHWARZ J. & WÓJCICKI J.J. 2002. The predominantly aquatic flora from Pellendorf, Lower Austria, Late Miocene, Pannonian – a systematic study. Acta Palaeobot., 42(2): 125–151.
- KRÄUSEL R. & WEYLAND H. 1950. Kritische Untersuchungen zur Kutikularanalyse tertiärer Blätter 1. Palaeontographica, B, 91: 7–92.
- KRÜSSMANN G. 1983. Handbuch der Laubgehölze, 2nd ed. P. Parey, Berlin, Hamburg.
- KRUTZSCH W. 1967. Der Florenwechsel im Alttertiär Mitteleuropas auf Grund von sporenpaläontologischen Untersuchungen. Abh. Z. Geol. Inst., Paläont. Abh., 10: 17–37.
- KRUTZSCH, W. unter Mitarbeit von BLUMENSTENGEL H., KIESEL Y. & RÜFFLE L. 1992. Paläobotanische Gliederung des Alttertiärs (Mittelozeän bis Oberoligozän) in Mitteldeutschland und das Problem der Verknüpfung mariner und kontinentaler Gliederungen. N. Jb. Geol. Paläont., Abh., 186(1, 2): 137–253.
- KUNZMANN L. 1995. Rekonstruktion einer tertiären Flusslandschaft. Abh. Staatl. Mus. Mineral. Geol. Dresden, 41: 73–95.
- KUNZMANN L. 1997. *Trigonobalanopsis* Kvaček & Walther, *Alnus* Miller und *Salix* Linné im Unteroligozän Nordwestsachsens. Abh. Staatl. Mus. Mineral. Geol. Dresden, 43/44: 227–237.
- KUNZMANN L. & WALTHER H. 1997. How to reconstruct a riparian environment?: methods, problems, results. In: Herengreen G.F.W. (ed.) Proceedings of the 4th European Palaeobotanical Palynological Conference. Mededelingen Nederlands Instituut voor Toegepaste Geowetenschappen TNO, 58: 219–225.
- KVAČEK Z. 1994. Connecting links between Arctic Palaeogene and European Tertiary floras. In: Boulter M.C. & Fischer H.C. (eds) Cenozoic plants and climates of the Arctic. Arcto-Tertiary Conf. London. NATO ASI Ser. 1, 27: 251–266.
- KVAČEK Z. & SAKALA J. 1999. Twig with attached leaves, fruits and seeds of *Decodon* (Lythraceae) from the Lower Miocene of northern Bohemia, and implications for the identification of detached leaves and seeds. Rev. Palaeobot. Palynol., 107: 201–222.
- KVAČEK Z. & WALTHER H. 1989. Revision der mitteleuropäischen tertiären Fagaceae nach blattepidermalen Charakteristiken, 3. Teil. *Dryophyllum* Debey ex Saporta and *Eotrigonobalanus* Walther & Kvaček gen. nov. Feddes Repert., 100(11–12): 575–601.
- KVAČEK Z. & WALTHER H. 1998. The Oligocene volcanic flora of Kundratice near Litomerice, České Středohoří volcanic complex (Czech Republic) – a review. Acta Mus. Nat. Pragae, Ser. B, Hist. Nat., 54(1–2): 1–42.
- KVAČEK Z. & WALTHER H. 2001. The Oligocene of Central Europe and the development of forest vegetation in space and time based on megafossils. Palaeontographica, B, 259(1–6): 125–148.
- MAI D.H. 1995. Tertiäre Vegetationsgeschichte Europas, Methoden und Ergebnisse. G. Fischer, Jena.
- MAI D.H. & WALTHER H. 1978. Die Floren der Haselbacher Serie im Weißelster-Becken (Bezirk Leipzig, DDR). Abh. Staatl. Mus. Mineral. Geol. Dresden, 28: 1–200.
- MAI D.H. & WALTHER H. 1983. Die fossilen Floren des Weißelster-Beckens und seiner Randgebiete. Hall. Jb. Geowiss., 8: 59–74.
- MAI D.H. & WALTHER H. 1985. Die obereozänen Floren des Weißelster-Beckens und seiner Randgebiete. Abh. Staatl. Mus. Mineral. Geol. Dresden, 33: 1–260.
- MAI D.H. & WALTHER H. 1991. Die oligozänen und untermiozänen Floren NW-Sachsens und des Bitterfelder Raumes. Abh. Staatl. Mus. Mineral. Geol. Dresden, 38: 1–230.
- NIKITIN P.A. 1929. The systematic position of the fossil *Diclidocarya* E.M. Reid. J. Bot., 57: 33–38.
- RASCHER J., ESCHER D., FISCHER J., DUTSCHMANN U. & KÄSTNER S. 2005. Geologischer Atlas Tertiär Nordwestsachsen 1 : 250 000. In: Standke G. (ed.) Sächs. Landesamt für Umwelt u. Geologie, Dresden.
- REID E.M. 1920. Recherche sur quelques graines pliocènes du Pont-de-Gail (Cantal). Bull. Soc. Géol. Fr. Ser. 4, 20: 48–87.
- ROSSMÄSSLER E.A. 1840. Die Versteinerungen des Braunkohlensandsteines aus der Gegend von Altsattel in Böhmen (Ellbogener Kreis). Arnoldsche Buchhandl., Dresden, Leipzig.
- RÜFFLE L., MÜLLER-STOLL W.R. & LITKE R. 1976. Weitere Ranales, Fagaceae, Loranthaceae, Apocynaceae. Abh. Z. Geol. Inst., Paläont. Abh., 26: 199–282, Tafelband Pl. 19–39.
- STERNBERG, K. v. 1823. Versuch einer geognostisch – botanischen Darstellung der Flora der Vorwelt, 3. Ernst Brenck's Wittwe, Regensburg.
- TAKHTAJAN A. L. 1996. Diversity and classification of flowering plants. Columbia University Press, New York.
- UNGER F. 1850. Genera et species plantarum fossilium. W. Braumüller, Wien.
- WALTHER H. 1990. The Weisselster-Basin (GDR) – an example of the development and history of the Palaeogene forest vegetation in Central Europe:

149–158. In: Knobloch E. & Kvaček Z. (eds) Proceedings of the Symposium Palaeofloristic and Palaeoclimatic changes in the Cretaceous and Tertiary. Geol. Surv., Prague.

WALTHER H. 1994. Invasion of arcto-tertiary elements in the Paleogene of Central Europe. In: Boulter M.C. & Fischer H.C. (eds) Cenozoic plants and climates of the Arctic. Arcto-Tertiary Conf. London. NATO ASI Ser. 1, 27: 239–250.

WALTHER H. & KUNZMANN L. (in prep.). Einmalige Blattfloren aus den oberoligozänen Thierbacher Schichten im ehemaligen Tagebau Bockwitz bei Borna (Freistaat Sachsen, Deutschland).

PLATES

Plate 1

1. Sediment block MMG PB Schle MO 556, from the open cast mine "Vereinigtes Schleenhain" near Borna, Saxony, Germany, Haselbach Member, Borna Formation, lowermost Lower Oligocene
2. Detail of the above block showing a mass accumulation of *Apocynophyllum nerifolium* Heer 1861 emend., short shoots of *Taxodium dubium* (Sternberg 1823) Heer 1855, and wood fragments

Scale bar (square) – 1 cm

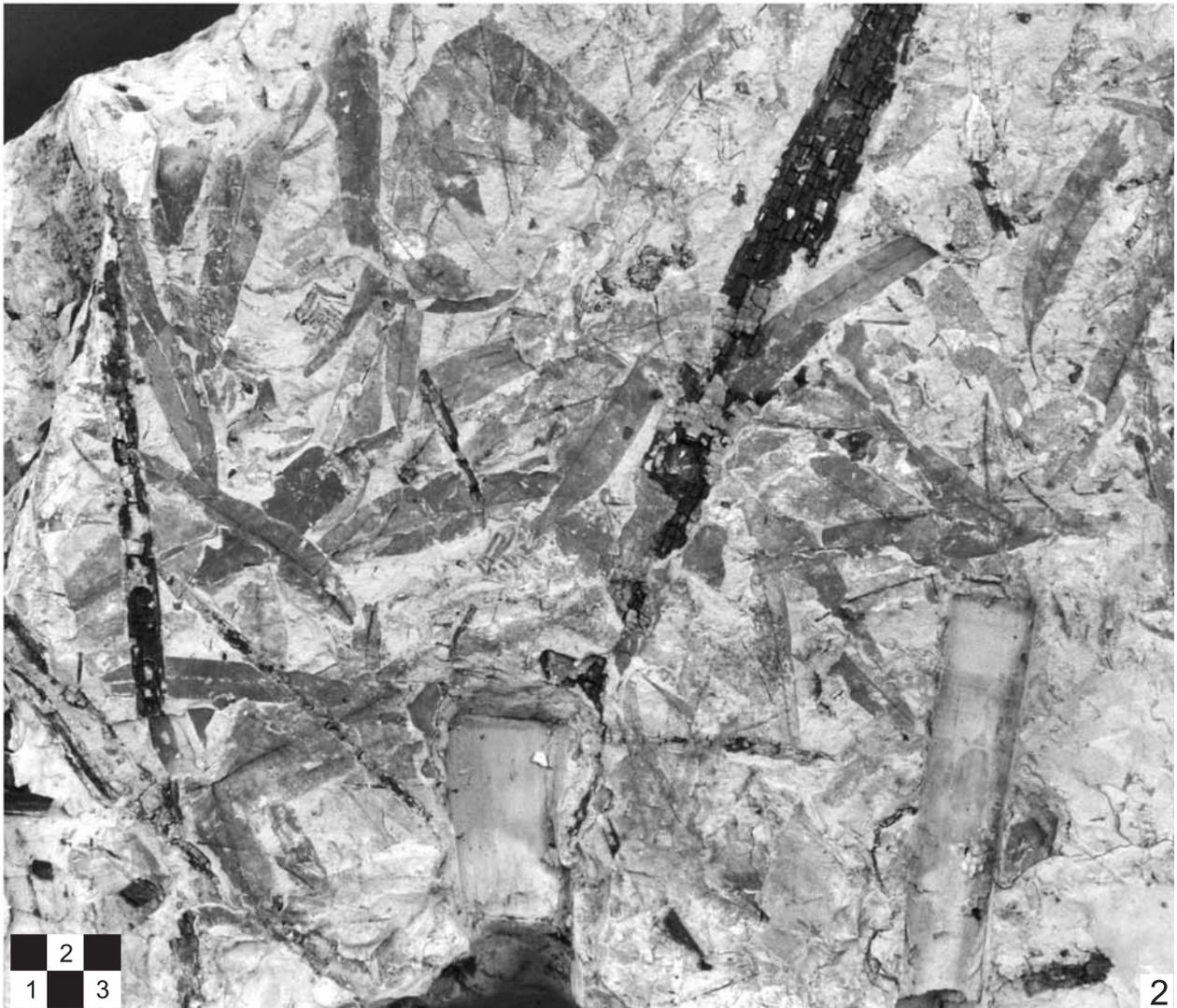
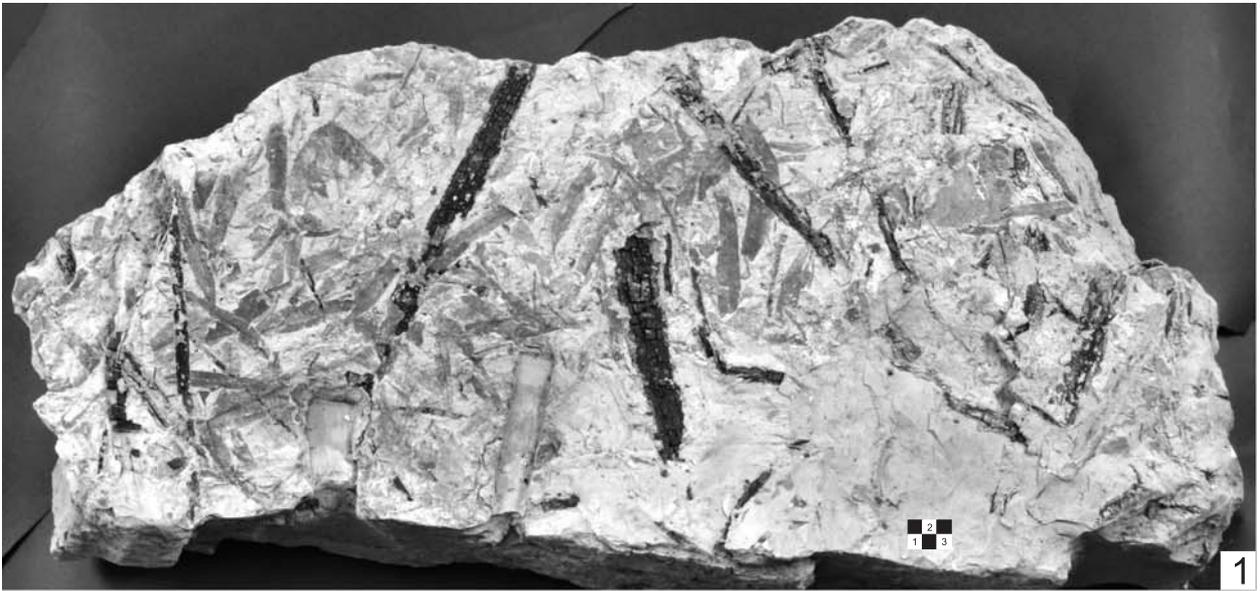


Plate 2

Apocynophyllum neriifolium Heer 1861 emend. based on material from sediment block MMG PB Schle MO 556, open cast mine "Vereinigtes Schleenhain" near Borna, Saxony, Germany, Haselbach Member, Borna Formation, lowermost Lower Oligocene

1. Small narrow leaf lamina (X), Schle MO 556 : 147; longest leaf (100 mm), curved lamina (XX), Schle MO 556 : 140
2. Leaves and leaf fragments together with short shoots of *Taxodium dubium* (Sternberg 1823) Heer 1855 (X)
3. Leaf showing cuneate base and petiole, Schle MO 556 : 101
4. Leaf, source of cuticles figured in Pl. 3, Schle MO 556 : 4
5. Leaf venation, Schle MO 556 : 93
6. Detail of fig. 5 showing intersecondary veins, intramarginal vein and higher venation
7. Taphonomic aspect: leaf, abaxial side up, Schle MO 556 : 93
8. Taphonomic aspect: leaf, adaxial side up, Schle MO 556 : 16

Scale bar (square) – 1 cm

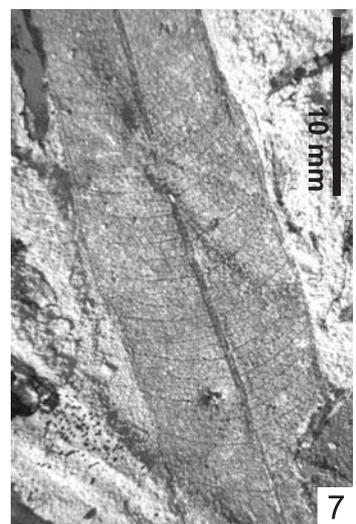
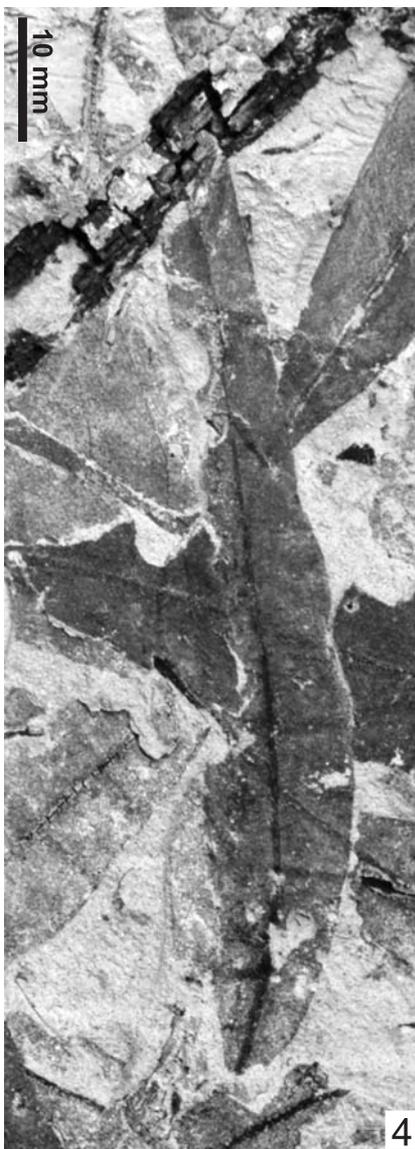


Plate 3

Apocynophyllum neriifolium Heer 1861 emend.

- 1–4. Leaf cuticles, open cast mine “Vereinigtes Schleenhain” near Borna, Saxony, Germany, Haselbach Member, Borna Formation, lowermost Lower Oligocene, Schle MO 556 : 4
1. Abaxial cuticle showing anomocytic stoma, sinuous anticlinal walls of ordinary epidermal cells, rectangular cells beneath veins, and epicuticular relief (wrinkles, striae). Preparation slide Schle MO 13/05, interference contrast
 2. As fig. 1, phase contrast
 3. Abaxial cuticle showing anomocytic stomata. Preparation slide Schle MO 14/05, interference contrast
 4. Adaxial side with fungal hyphae. Preparation slide Schle MO 13/05, interference contrast
- 5–8. Leaf cuticle, original Mai & Walther 1978: pl. 47, fig. 2, open cast mine “Haselbach” near Borna, Saxony, Germany, Haselbach Member, Borna Formation, lowermost Lower Oligocene. Preparation slide Hb 209/69 of leaf Hb 315a
5. Adaxial cuticle showing epicuticular relief (wrinkles, striae), phase contrast
 6. Abaxial cuticle showing anomocytic stomata and epicuticular relief (wrinkles, striae), interference contrast with oil
 7. As fig. 6, overview, interference contrast
 8. As fig. 6, overview, phase contrast

