Acta Palaeobotanica 47(1): 217–235, 2007

Magnolia L. in peat-forming associations of the Miocene seams in Lower Lusatia (East Germany)

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Received 31 July 2006; accepted for publication 9 December 2006

ABSTRACT. The autochthonous humodile – taphocoenoses in the 2nd seam (middle Miocene) of Lusatia (Nochten mine) include numerous remains of leaves, seeds and fruits, additional sporomorphs, antheres and wood fragments. The most common leaf taxon has been described as *Papilionaceophyllum liblarense* Kräusel & Weyland, whereas the likewise predominant carpological taxon belongs to *Carpolithus burseraceus* Menzel. Combinations of both epithets with the genus *Magnolia* L. by Kvaček respectively Mai indicate an occurrence of two *Magnolia* species for the association under discussion. The taphonomic results point to the presence of a single species of *Magnolia* L. The taxonomic aspect of this fact is explained. Based on numerous specimens, new results concerning morphology and anatomy of leaves and seeds are described. *Magnolia* remains characterize a distinct stage ("A-facies") of palustric successions in association with *Kalmiophyllum marcodurense* Kräusel & Weyland and *Quercus rhenana* (Kräusel & Weyland) Knobloch & Kvaček. The characters of *Magnolia* leaf fossils remain constant throughout the Neogene of Central Europe uninfluenced by climatic changes. Likewise the indication of telmatic conditions is reliable.

KEY WORDS: fossil *Magnolia*, leaf anatomy, cuticular analysis, Miocene, Lusatia, Germany

INTRODUCTION

Leaf-bearing seam strata occur within the 2nd Lusatian seam horizon (middle Miocene). In the open cast mine Nochten (Fig. 1) the taphocoenoses "NQ 93" and "NQ 96" have been examined (Schneider 2004). The specimens described in the present paper are members of the taphocoenosis "NQ 96" (Figs 2, 3), which represents the "Angiosperm facies (A)" in the middle layer of the 2nd Lusatian seam horizon. The plant fossils are components of a well-bedded dark brown coal rich in humified plant tissues and poor in ash. Leaves and seeds are well preserved and do not show influences of transport. The plant cuticles are in an excellent preservational state. Main components of the taphocoenosis NQ 96 are leaves and seeds belonging to the genus *Magnolia* L.

For understanding the taphocoenoses included in the middle Miocene 2nd seam of Lusatia it is necessary to compare peat-forming plant assemblages from younger and older Miocene seams and some results known from Upper Eocene seams in the Weißelster Basin. The *Magnolia* leaves described from Palaeogene are rarely (Walther 2003) and don't permit evidences about variation and correlation of characteristics. On the other hand, a phylogenetic interpretation of epidermal characteristics given for leaves from Middle Eocene Geiseltal – seams (Rüffle et al. 1976) may be important for a comparison with the Miocene *Magnolia* remains.

The specimens and preparations for description and illustration are deposited in the collection of the author. Specimens of the taphocoenosis NQ 96 have been handed to the Museum for Mineralogy and Geology of the State Natural History Collections Dresden, the Natural History Museum at the Humboldt University Berlin and the Museum for Nature and Environment in Cottbus.

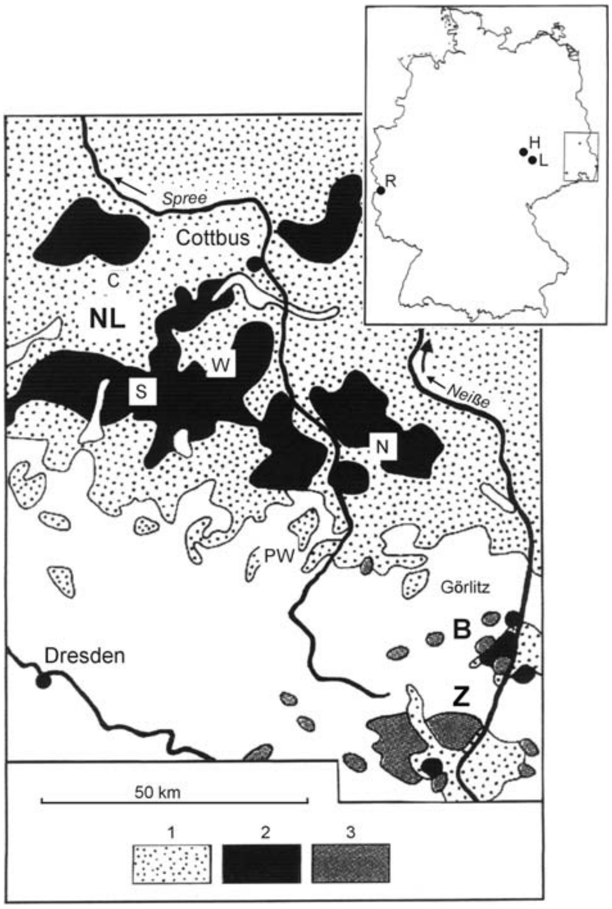

Fig. 1. Distribution of seam-bearing Miocene deposits of Lower Lusatia (**NL**) showing important locations of described leaf fossils and taphocoenoses: **N** – Nochten mine (taphocoenoses NQ 96 and NQ 93), **W** – Welzow mine, **S** – mines around of Senftenberg, **PW** – closed mines at Puschwitz – Wetro, **C** – Calau: location indicating Calau beds (Lower Oligocene), **H** – Halle and **L** – Leipzig: locations indicating occurrences of *Magnolia* leaf remains in Upper Eocene coal seams. **B** – Berzdorf basin, **Z** – Zittau – Turów basin, **R** – Lower Rhine Basin, **1** – area of Neogene sediments, **2** – area of lignite mining, **3** – volcanic rocks (basalt, phonolite, tuff). According to Henningsen & Katzung (1998)

DESCRIPTION OF THE PLANT FOSSILS

Genus ***Magnolia*** L.

Leaf remains showing morphologic and microscopic characteristics

Morphospecies ***Papilionaceophyllum liblarense*** Kräusel & Weyland 1959

Figs 2–4; Pl. 1, fig. 9, Pl. 2, figs 1, 2

Cuticulae dispersae

Morphospecies ***Falcicutis varians*** Schneider 1969

Pl. 1, figs 1–8

1939 Cuticle from Laubblatt sp. E, Mädler pl. 13, figs 7–9.
1958 cf. *Laurophyllum*, Neuy-Stolz, pl. 7, fig. 5.
1959 *Papilionaceophyllum liblarense* n. sp. Kräusel & Weyland, p. 111–114, pl. 24, figs 38–41, pl. 25 figs 42–47, pl. 26, fig. 48, taxt.-fig. 11.
1963 *Cynometrophyllum villense* n. sp. Weyland & Kilpper, p. 109–110, pl. 29, figs 52–56.
1966 *Papilionaceophyllum liblarense* Kräusel & Weyland; Litke, p. 373–374, pl. 25, figs 3, 4, text-fig. 13a,b,d.
1966 *Papilionaceophyllum liblarense* Kräusel & Weyland; Schneider, pl. 6, fig. 19.
1966 Kutikula incertae sedis NFu 15, Litke, p. 373–374, pl. 29 figs 5, 6, text-fig. 18b.
1967 Kutikula incertae sedis NFu 15, Litke, pl. 3, fig. 11.
1967 *Papilionaceophyllum liblarense* Kräusel & Weyland; Weyland et al., p. 156, text-fig. 18.
1969 *Falcicutis varians* n. fsp., Schneider, pl.5, figs 3–5, pl. 6, figs 1–6, text-fig. 3.
1973 *Falcicutis aperta* n. fsp., Schneider, pl. 1, figs 6, 7; pl.2, figs 1, 2, text-fig. 7.
1975a *Papilionaceophyllum liblarense* Kräusel & Weyland; Givulescu, pl.1, figs 7,8, pl. 2, fig. 6, pl. 3, fig. 7, pl. 4, fig. 7.
1975b *Papilionaceophyllum liblarense* Kräusel & Weyland; Givulescu, pl. 20.
1978 *Magnolia liblarensis* (Kräusel & Weyland) comb. n., Kvaček, pl. 37, figs 2–5.
1992 *Magnolia liblarensis* (Kräusel & Weyland) Kvaček (*Falcicutis varians*); Schneider, pl. 2, figs 6, 7.
1996 *Magnolia liblarensis* (Kräusel & Weyland) Kvaček; Knobloch & Kvaček, pl. 4, fig. 6.
1996 *Magnolia liblarensis* (Kräusel & Weyland) Kvaček; Erdei, p. 91, pl. 3, figs 12–13.
2001 *Magnolia liblarensis* (Kräusel & Weyland) Kvaček; Kovar-Eder et al., fig. 4.
2001 *Magnolia liblarensis* (Kräusel & Weyland) Kvaček; Kovar-Eder & Meller, p. 72, pl. 4, 5, pl. 3 fig. 3.
2004 *Falcicutis varians* Schneider; Schneider, pl. 1, fig. 7, text-fig. 17.

Leaves microphyllous. Length 6 (2–11) cm, width 2 (1–4) cm. Lamina 6–15 cm^2. Leaf shape elliptic. Apex acute or obtuse rarely acuminate, base acute. Margin entire (Figs 2, 4). Drip tips (Fig. 2A) rarely occur on broad leaves. Petiole up to 2.5 cm in length (Figs 2, 4).

Leaves chartaceous. The cuticle of both surfaces is thin (Pl. 1, fig. 7, Fig. 5H) and does not show xerophytic adaptations. Surface ornamentations and papillae are absent. In some cases the cuticular layers forming the anticlinal walls are peeled off. The remaining outer layer (cuticle sensu stricto) appears structureless and shows only the basal cells of trichomes (Pl. 1, fig. 7).

Fig. 2. *Papilionaceophyllum liblarense* Kräusel & Weyland. Leaf morphology. Specimens from the 2nd seam horizon (middle layer 2) of Nochten (Lusatia): **A** – NQ 9621, **B** – NQ 9641, **C** – NQ 9636, **D** – NQ 9658, **E** – NQ 9749, **F** – NQ 9820, **G** – NQ 9793, **H** – NQ 9607, **I** – NQ – 9637, **J** – NQ 9821, **K** – 9800, **L** – 9656, **M** – NQ 9750, **N** – NQ 9602, **O** – NQ 9660, **P** – NQ 9729, **Q** – NQ 9801, **R** – NQ 9661. Numbers on the leaf drawings: on the right – stomata frequency (s/1mm^2), italics on the left – trichome frequency (t/1mm^2). Specimens from the Main seam of the Lower Rhenish Basin: **S**, **T**, **U**, **V**, **W**, **X** after Kräusel & Weyland (1959) **T** – Type specimen SM. B. 8456/1, l.c. fig. 10 pl. 24, fig. 39, **Y** – after Weyland et al.(1967 fig. 18)

Fig. 3. Composition of the taphocoenosis NQ 96 dominated by *Papilionaceophyllum liblarense* from the 2nd seam horizon in the Nochten mine (Lusatia). The graph shows the quantity of the constituents. The direction of leaves and shoots is incidental. Leaves without designation – *Papilionaceophyllum liblarense* Kräusel & Weyland **Km** – *Kalmiophyllum marcodurense* Kräusel & Weyland (Ericaceae), **Kt** – *Kalmiophyllum tectirimum* Schneider (Ericaceae), **Mg** – *Viscophyllum miqueli* f. *parvula* Rettschlag 1954 (*Viscum*), **Qr** – *Quercus rhenana* (Kräusel & Weyland 1951) Knobloch & Kvaček 1976, **Lr** – leaves with cuticular structure *Lusaticutis rugosa* Schneider (cf. Cyrillaceae), **Pht** – *Phyllites thomsonii* (Kräusel & Weyland 1954) Schneider (Cyrillaceae), **Kl** – *"Illicium" lusaticum* (Jähnichen 1954) Kräusel & Weyland (Dicotyledonae incertae sedis), **Vl** – leaves with cuticular structure *Varipilicutis liblarensis* (Kräusel & Weyland 1954) Schneider (Zingiberaceae vel Pontederiaceae), **Sq** – *Sequoia abietina* (Brongniart in Cuvier 1822) Knobloch 1964, **Tw** – *Taiwania schaeferi* Schloemer-Jäger 1958, **Pi** – *Pinus* cf. *rigios* (Unger 1852) Ettingshausen 1866 sensu Mai 1999a with cuticular structure *Pinicutis hexacytica* Schneider, **Mb** – *Carpolithus burseraceus* Menzel

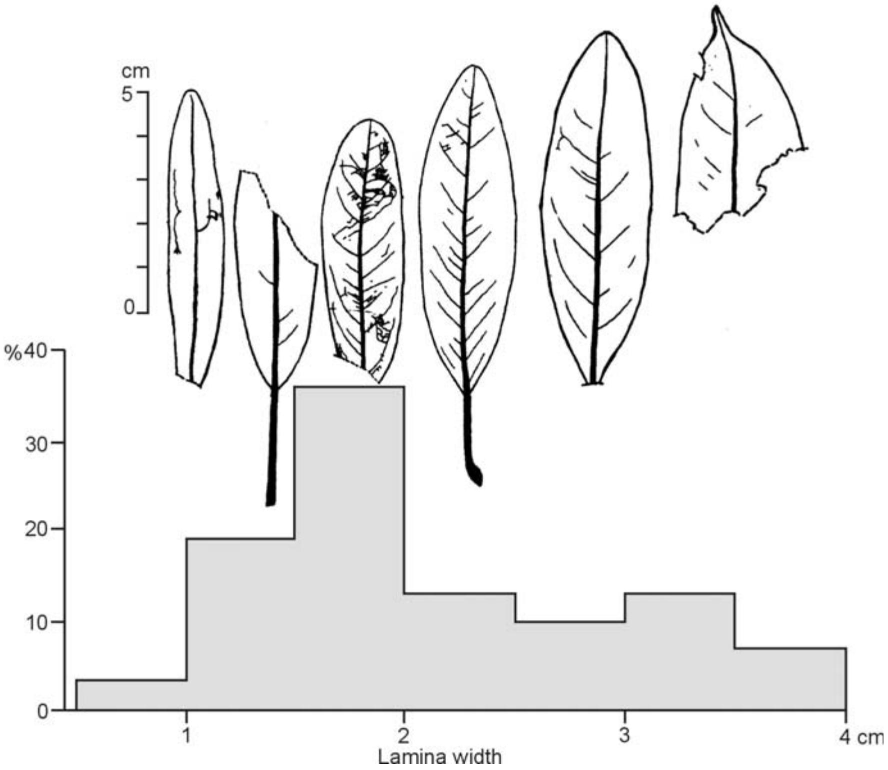

Fig. 4. *Papilionaceophyllum liblarense* Kräusel & Weyland from the Nochten NQ 96 taphocoenosis. Leaf size and its distribution, related to leaf width as mostly measurable characteristic

The adaxial surface of the leaves shows a knoblike relief caused by secretory bodies (Pl. 2, fig. 2), whereas the abaxial surface is covered by a white layer consisting of wax (Pl. 2, figs 1, 2). The leaf venation is extensively described by Kräusel & Weyland (1959) and Kvaček (1978). The primary vein is stout and of straight course. The number of secondaries is 8 to 12 (Fig. 2).

The adaxial cuticle is divided into veins and intercostal areas (Pl. 1, figs 1, 2). Stomata and trichomes are lacking. Anticlinal walls were described as straight (Kräusel & Weyland 1959, Kvaček 1978) or undulate (Schneider 1969, pl. 5, fig. 3). In the Nochten taphocoenosis the cuticles of broad leaves show straight cell walls whereas the anticlines of narrow leaves (as Fig. 2F) are undulate.

The abaxial cuticle is divided into veins and intercostal areas (Pl. 1, figs 3–7). Stomata restricted to intercostal areas, randomly arranged. Trichome bases on veins and in intercostals areas. Anticlinal walls are straight to undulate without any correlation to leaf morphology.

In some cases a hypodermis was found below the adaxial surface (Pl. 1, fig. 1). The cellareae (Roselt & Schneider 1969) of the hypodermis are of rectangular shape with hexagonal arrangement and about 230 × 80 µm in size. One cellarea of the hypodermis includes 20–30 cellareae of the epidermis. The anticlinal walls are straight in contrast to the undulate epidermal walls. A hypodermis in Magnoliaceae is often differentiated (Baranova 1972).

Stomata are restricted to the abaxial surface of leaves. Guard cells and lateral neighbouring cells may be distinguished. The stomata in their topographic aspects correspond to the paracytic type according Metcalfe and Chalk (1957) respectively to the brachyparacytic type according to Dilcher (1974). The stomata are not sunken. The cuticle covering the guard cells is thinner than on the subsidiary cells (Pl. 1, fig. 5). The spindle-shaped stomatal aperture is mostly indistinct because stomatal ledges are missing. Likewise T-pieces are not developed at the stomatal poles.

Neighbouring cells bordering on guard cells are named as subsidiary cells. Encircling cells follow in distal direction. They are somewhat thicker than the guard cell cuticle. Between subsidiary and guard cell an anticlinal wall is lacking. The surface form of subsidiary cells is narrow sickle-shaped. The subsidiary cells do not surround the guard cells completely. Therefore, a single polar neighbouring cell occurs in the vicinity of the stomatal pole. Transverse divisions of subsidiary cells, as observed on *Magnolia liliiflora* Desr. are lacking. Longitudinal divisions yield encircling cells. The outlines are mostly recognizable on immature stomata (Pl. 1, fig. 4; Fig. 5B). However, in the vicinity of mature stomata encircling cells in most cases cannot be distinguished from normal epidermal cells.

The average length of the stomata lies between 20–23 µm. Heterostomata (water-stomata) about 25 µm in size occasionally occur.

Trichomes occur only on the abaxial sur-

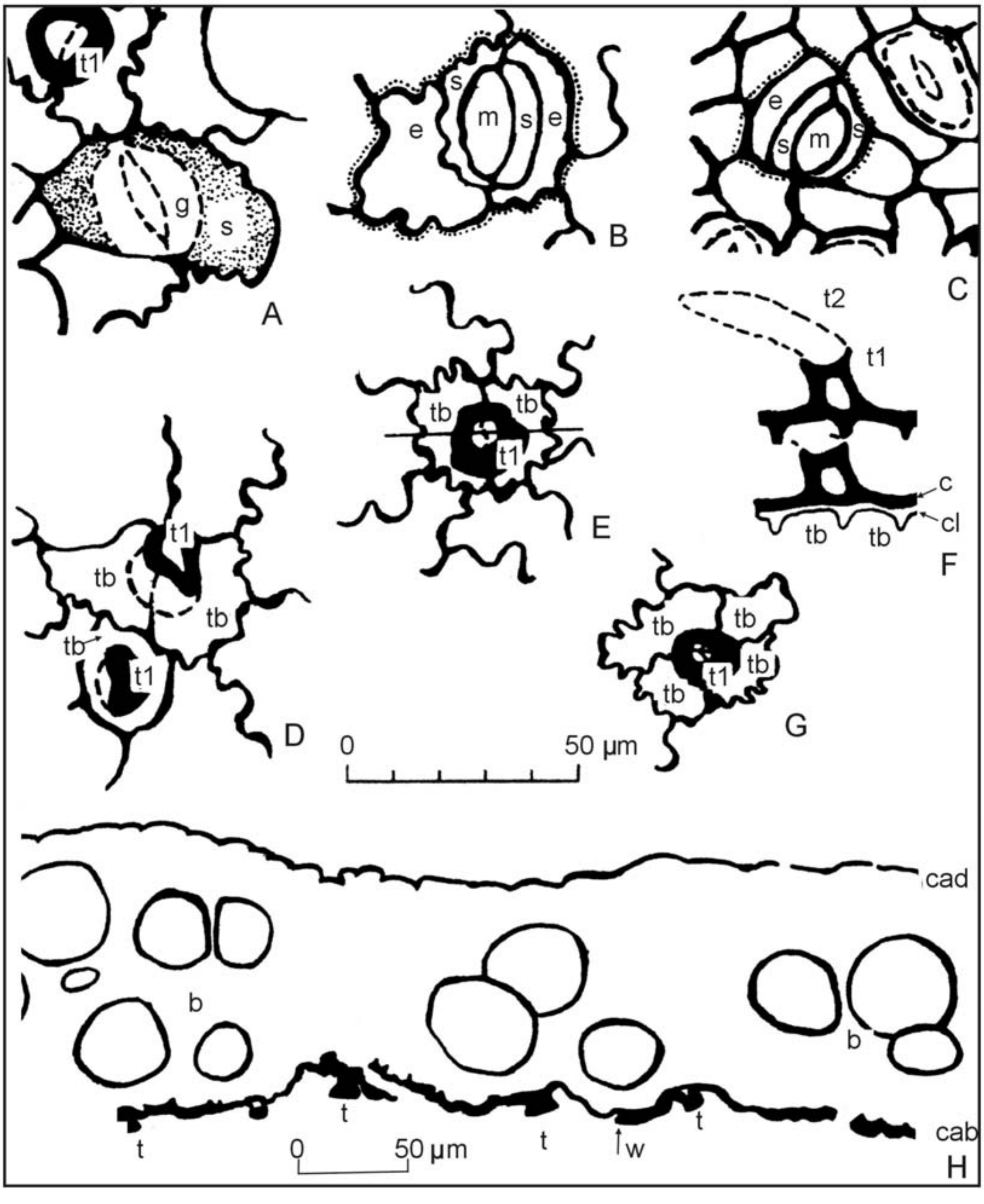

Fig. 5. *Papilionaceophyllum liblarense* Kräusel & Weyland respectively *Falcicutis varians* Schneider. Anatomical characteristics. **A** – stoma abnormal in width, showing the different thickness of cuticle covering guard cells (**g**) and subsidiary cells (**s**). No thickenings developed around the stomatal aperture and near the stomatal pole. Trichome (**t1**) directly adjoining on a 2- celled base. **B** – immature stomatal apparatus showing the stages of ontogeny: the "given protoderm cell" (Esau 1953, outline dotted) is divided threetimes. The last division forms two doughter cells different in size (inequal division). The smaller cell acts as stomatal initial = guard mother cell (**m**). The remaining cells become encircling cells (**e**) and subsidiary cells (**s**). Miocene seam, Wetro mine, Upper Lusatia, Prep. IBG 248. **C** – as B. Upper Eocene seam, Etzdorf mine near Halle, Prep. IBG 424. **D**, **E**, **F**, **G** – trichomes. Basal cell of trichome (**t1**) mounted on one (D), two (D, E, F) and four trichome base cells (**tb**). **F** – Section-view showing basal (**t1**) and terminal (**t2**) cell of the trichome (above) and affiliation of the trichome to the cuticle in strict sense (**c**). cl = cuticular layer. 1st Miocene seam, Welzow mine, Prep. 1783. **H** – section of leaf showing adaxial (**cad**) and abaxial (**cab**) cuticle. Abaxial cuticle with trichomes (**t**) an layers of wax (**w**). Internal secretory bodies (**b**) of spherical shape. Drawing after photo under fluorescence conditions (reflecting light). 2nd Miocene seam, Nochten mine, Prep. NQ 96b

face. The frequency differs between absence and very dense arrangement. Trichome bases are 1- to 4-celled as Kvaček (1978) recognized (Pl. 1, figs 5–7; Fig. 5D–H). Trichomes consist of two cells (Fig. 5F). The basal cell (t1) is anvil-shaped and always preserved. The thick cell wall is formed from the outer layer of the cuticle (cuticle in strict sense). The cuticular layers forming the anticlinal walls resp. the "cellimites" (Roselt & Schneider 1969, fig. 2) did not participate in the development of the trichome cells. The terminal cell is very rarely preserved. Only one cuticle with complete trichomes has been found in the Lusatian localities (Puschwitz-Wetro basin, Upper Lusatia, Schneider 1966). There, the terminal cell is of cylindrical shape with a rounded apex and its cuticle is thin-walled without protuberances. Of the few thousand cuticle fragments from the Miocene seams of Lower Lusatia none shows a terminal cell. This condition most probably excludes an occurrence of terminal trichome cells even in juvenile leaves thus indicating the ontogenetic reduction due to growth in wet environments.

One of the most peculiar features of the present leaf fossils is the rich occurrence of secretory bodies of 50 µm in size. They are included in oil cells embedded in the mesophyll and show a dark coloured core. The cell pattern of the leaf epidermis does not show apertures or other anomalies. Often the resin bodies are impressed into the cuticle by compaction of the surrounding organic matter. In reflecting light microscopy they are known as "soft brownish" resinite bodies showing dark yellow emission under blue light (Pl. 1, fig. 9).

Seed remains

Carpolithus burseraceus Menzel 1913

Pl. 2, fig. 3

1913 *Carpolithus burseraceus* Menzel, pl. 7, figs 10–12.
1975 *Magnolia burseracea* (Menzel) n.comb., Mai, pl. 35, figs 24–26.
1997 *Magnolia burseracea* (Menzel) Mai; Mai, description p. 25, without figs.
1999b *Magnolia burseracea* (Menzel) Mai; Mai, pl. 1, figs 7–12.
2004 *Carpolithus burseraceus* Menzel; Schneider, pl. 14, figs. 1–3, text-fig. 4.

In the taphocoenosis NQ 96 10 seeds have been found. Seeds 5–7.5 mm long and 4–6 mm broad, rounded, partly heart-shaped. Surface smooth. The characteristics correspond to the description given by Mai (1997). In the present taphocoenosis the seeds are surrounded by a layer about 1 mm thick representing the sarcotesta. This tissue contains densely arranged spherical secretory bodies of 60–140 µm in diameter (Pl. 2, fig. 3). The honey-coloured bodies include a dark core.

DISCUSSION

The leaves from the Nochten taphocoenosis NQ 96 are somewhat smaller than the dimensions given in Kvaček (1978). *Papilionaceophyllum liblarense* Kräusel & Weyland may be compared with small-leaved magnolias as *Magnolia virginiana* L. with leaf size up to 6.5–10.5 × 3.5–4.5 cm (Tobe 1998). The length of the pedicellus (up to 2.5 cm, about a quarter of the leaf length) seems to be characteristic of the present leaf fossils.

The stomatal complexes are situated in the level of the epidermis. This organisation has been mainly observed in deciduous *Magnolia* species growing in swamp regions. Contrastingly in some evergreen magnolias as *M. grandiflora* L., *M. splendens* Urb. (Pl. 2, fig. 6), and *M. domingensis* Urb. the stomata are sunken and partly covered by papillae.

On the abaxial cuticle immature stomatal complexes may occasionally be observed (Fig. 5B, C) revealing on ontogeny as described by Rao (1939) and Paliwal and Bhandari (1962) for Magnoliaceae. After three inequal divisions a meristemoid (Bünning 1953) develops into a guard mother cell. The remaining cells become encircling cells ("Kranzzellen" after Florin 1931) and subsidiary cells (Pl. 1, figs 4, 8; Fig. 5B, C). The encircling and subsidiary cells are defined as "mesogenous", because they result in the course of the meristemoid divisions. Due to the considerable density of stomata most "normal" epidermal cells on the abaxial surface must be regarded as encircling cells from their ontogeny.

The partition walls are not parallel to each other but convergent and as a rule U-shaped. This kind of ontogeny is different from the "syndetocheil" type of Florin (1933). Angular divisions as in the ontogeny of *Magnolia* stomata indicate the transition to the "Cruciferae-Typus" of Vesque (1885). The inequal divisions of the meristemoid cause lateral subsidiary cells of different size. The lateral subsidiary cells of *Papilionaceophyllum liblarense* are narrow. Therefore Kräusel and Weyland (1959) have misinterpreted the stomata as anomocytic. Subsidiary cells are recognizable in *Cynometrophyllum villense* (Weyland & Kilpper 1963) assigned to the present species by Kvaček (1978). Only a few living *Magnolia* species (*M. virginiana*, *M. schiedeana*) show narrow subsidiary cells.

The cuticular pattern of *Papilionaceophyllum liblarense* respectively *Falcicutis varians* is characterized by densely arranged stomata. In numerous cases two stomata are directly adjoined. According to Rao (1939) the stomatal frequency of Magnoliaceae is uniform over the leaf lamina. Counting of stomata reveals a complex pattern of relationships to morphological characters. On some leaves (Fig. 2A, F, H) the stomatal frequency increases from base to apex. Other leaves (Fig. 2K, Q) do not show any trend. On the other hand a distinct correlation was observed between stomatal frequency and leaf size. Leaves of average to small size (Fig. 2 F, K, Q) are characterized by 400 to >600 stomata/1mm^2. By comparison broad leaves (Fig. 2 A, B, H) show stomatal frequencies of <400 thus indicating shadow leaves.

Stomatal frequency as a function of stomatal size is depicted in Figure 6. In general, an increasing stomatal length is correlated to decreasing stomatal frequency. Stomatal sizes >35 µm are measured on thick leaves of evergreen species growing in the Carribean region and south-east of North America. *Papilionaceophyllum liblarense* from Nochten is arranged in the interval 20–25 µm in stomatal size together with *Magnolia virginiana* represented by a deciduous shrub in the forest garden of Tharandt (Saxony). *Magnolia "glauca"* (synonym of *M. virginiana* L.) growing in the Botanical Garden of Berlin as *M. schiedeana* Schlecht. from Mexican Sierra Madre are similar in stomatal frequency but show stomata of 25–30 µm in length.

The dependency between stomatal frequency and trichome frequency was not observed in the investigated fossil leaves. In general, leaves of average to small size (Fig. 2K, Q) show a dense cover of trichomes with a frequency of >100/1mm^2, whereas broad leaves are characterized by frequency <100 (Fig. 2 H, I) or by absence of

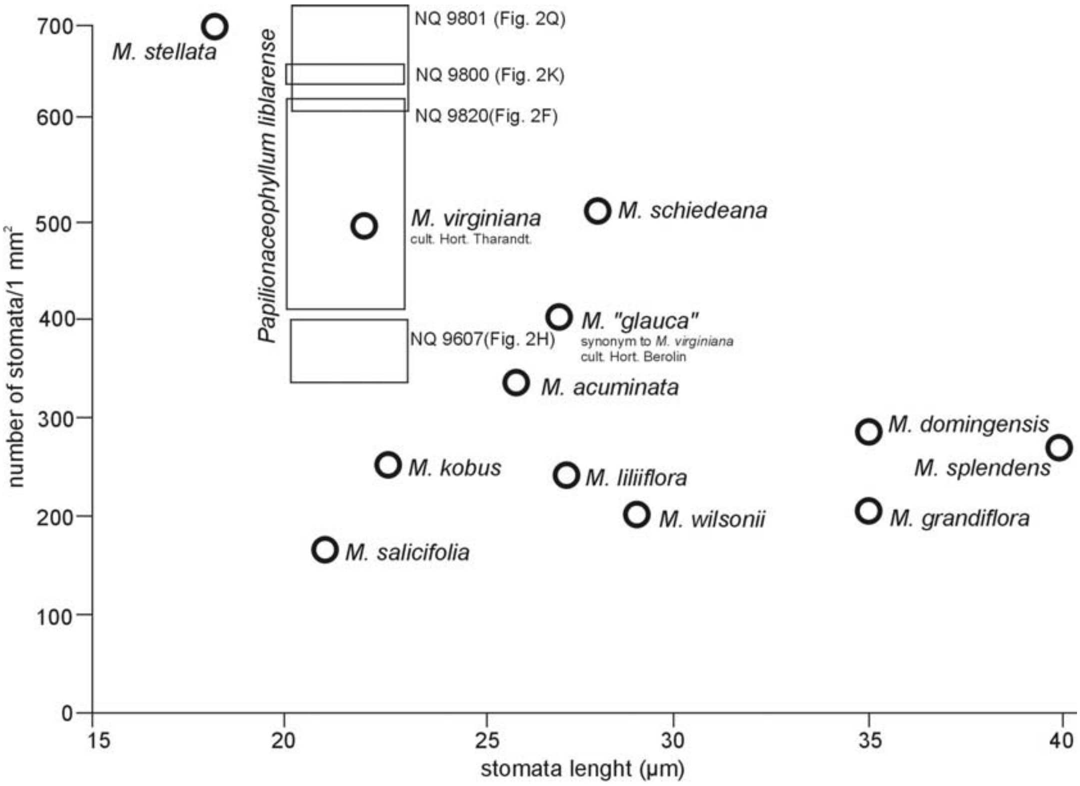

Fig. 6. Correlation between stomatal frequency and stomatal length of *Papilionaceophyllum liblarense*, compared with leaves from some modern *Magnolia* species. *Papilionaceophyllum*: measurements on apex, middle and base of four leaves from the taphocoenosis Nochten NQ 96. Modern species: measurement on the median part of one leaf (specimens from the herbarium of the Botan. Inst. Berlin-Dahlem and from living trees as noted)

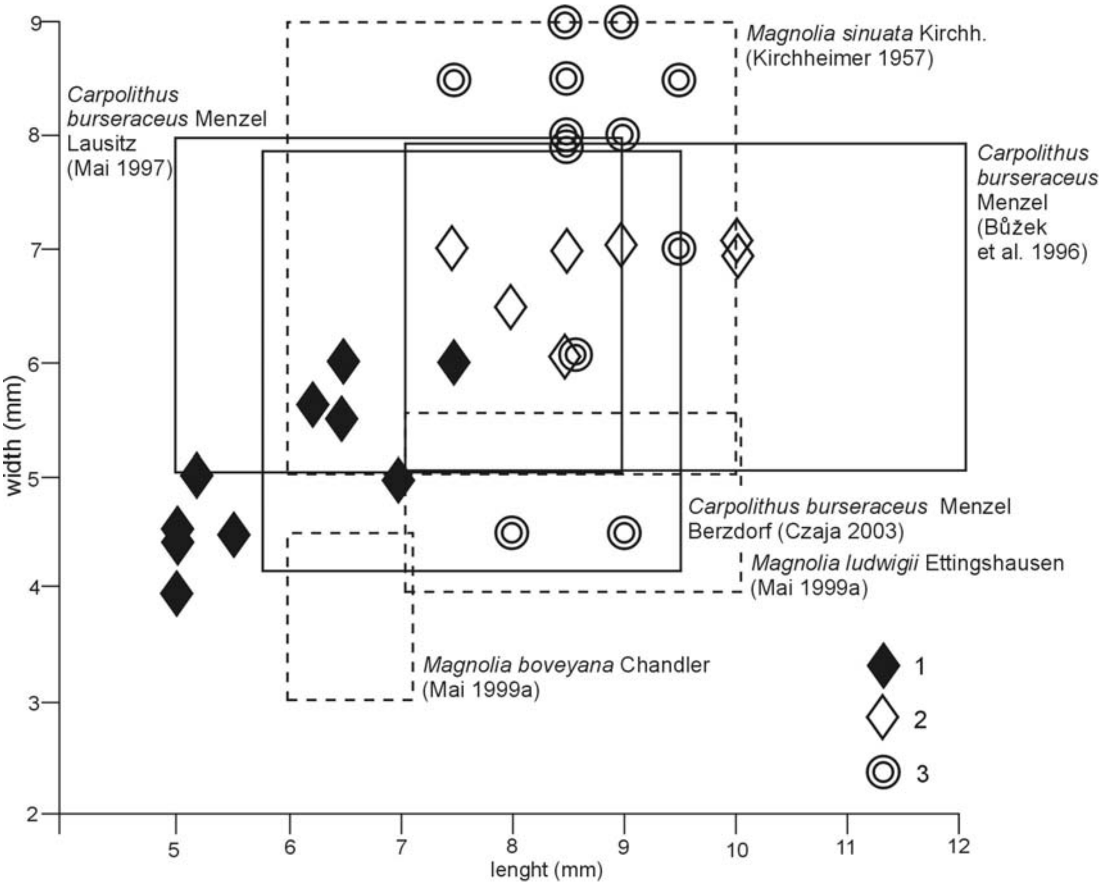

Fig. 7. *Carpolithus burseraceus* Menzel. Size of seeds from different Lusatian locations compared with intervals published for similar morphospecies. **1** – taphocoenosis Nochten NQ 96 (dominated by *Papilionaceophyllum liblarense*), **2** – taphocoenosis Nochten NQ 93 (dominated by *Kalmiophyllum tectirimum*, see Schneider 2004), **3** – 1st Lusatian seam specimens bearing numerous *Falcicutis varians*, clay pit Neukollm east of Senftenberg

trichomes (leaf showing drip tip, Fig. 2 A). In both cases exceptions occur (Fig. 2 B versus 2 F). The trichome frequency of living *Magnolia* species is not sufficiently investigated. Dense trichome covers are found on abaxial surface of leaves of *M. grandiflora* and *M. splendens. Magnolia virginiana* and *M. schiedeana* show 40 respectively 60 trichomes on 1 mm^2.

The carpologic species *Carpolithus burseraceus* Menzel is defined by measurements by Mai (1975). Intervals of 5–9 mm in length and 5–8 mm in width are appointed for Lusatian localities (Mai 1997). The populations described here (Fig. 7) are arranged in different parts of this field:

The seeds in the NQ 93 taphocoenosis dominated by *Kalmiophyllum tectirimum* (Schneider 2004) are 7–10 mm long and 5.5–7 mm broad.

The seeds in the NQ 96 taphocoenosis dominated by *Papilionaceophyllum liblarense* are smaller (5.5–7.5 mm long and 4–6 mm broad).

Seeds collected in the lower parts of the stratigraphic younger 1st Lusatian seam are similar to seeds from the NQ 93 population, but with large variation concerning the width.

TAXONOMY

Initially, by cuticular studies in brown coal seams Kräusel and Weyland (1959) determined some leaf fragments (Fig. 2 T–X) as type of a new organ genus *Papilionaceophyllum*. The interpretation of cuticular characteristics by the authors reveals some errors, which exclude an affinity to Papilionaceae (Schneider 1969). Kvaček (1978) proved the affinity of the fossils to the living genus *Magnolia* L. According to taxonomic rules the fossil leaves were named *Magnolia liblarensis* (Kräusel & Weyland) Kvaček. The epitheton "*liblarensis*" based on leaves occupies the status of a morphotaxon according Saint Louis Code 1999 Art. 1.2 (see Greuter et al. 2000). The new combination does not change this status. Moreover the new combination does not impart the presence of a morphotaxon.

The taxonomy of seed fossils found in the investigated taphocoenosis shows an analogous history. Mai (1975) proved the identity of seed fossils frequently occurring in Lusatian coal seams with *Carpolithus burseraceus* Menzel and assigned these fossils to the living genus *Magnolia* L.

The present studies on autochthonous taphocoenoses suggest, that with high probability *Magnolia liblarensis* (Kräusel & Weyland) Kvaček (leaves) and *Magnolia burseracea* (Menzel) Mai 1975 (seeds) represent the same species of *Magnolia* L. This whole plant is a hypothesis. The epitheta of the morphospecies are not suitable for designation of the whole plant. The morphotaxa based on corresponding nomenclatural types are related to fossil plant organs as the object of palaeobotanical research.

The taxonomic constellation described for *Magnolia* remains can be established in further examples from the autochthonous taphocoenoses in the Nochten locality:

Quercus rhenana (Kräusel & Weyland) Knobloch & Kvaček / *Quercus* spec. (?Sect. *Phellos* Loud.) Mai 1999b;

Clavaecutis lignita Schneider / *Nyssa disseminata* (Ludwig) Kirchheimer (see Schneider 2004).

The morphotaxon *Falcicutis varians* Schneider was established for dispersed cuticles. In the period between 1970 and 2000 a great quantity of samples, found in connection with brown coal exploration, were investigated for the purposes of coal seam modelling. The use of morphotaxa for dispersed cuticles is suitable for investigation of coal-bearing formations with large stratigraphic interval and regional extent.

MODERN ANALOGUES

The characteristics justifying the comparison of *Papilionaceophyllum* with the living genus *Magnolia* L. have been worked out by Kvaček (1978): stomata of paracytic mode, 2- to 4-celled trichome bases, trichomes showing multicellular file (1-cell thick), oil glands in the mesophyll. Kvaček (1978) found similar epidermal patterns e.g. in *Magnolia salicifolia* Buch. Ham. ex DC or *M. dealbata* Zucc.

On the basis of leaf size and morphology only a limited number of living *Magnolia* species are comparable to the fossil material. The most similar leaves are found in *Magnolia virginiana* L., which only differ by a shorter petiole (about 1/6 of the leaf length). Further corresponding characteristics are granular deposits of wax on the abaxial surface, stomatal size, stomatal frequency (Fig. 6), narrow sickle-shaped subsidiary cells and the position of stomata in the level of epidermis (not sunken, absence of papillae). Different is the absence of secretory bodies in *Magnolia virginiana* L.

Further living species differing in some characteristics from *Papilionaceophyllum liblarense*:

Magnolia schiedeana Schlecht.: leaves 12–16 × 5–7 cm, wax lacking;

Magnolia salicifolia (Sieb. & Zucc.) Maxim.: stomata partly sunken, subsidiary cells distinctive unequal, wax lacking;

Magnolia kobus DC: leaves 10–18 × 5–10 cm, subsidiary cells broad, wax lacking;

Magnolia acuminata L.: leaves 10–25 × 10–15 cm, stomata somewhat sunken.

Magnolia stellata (Sieb. & Zucc.) Maxim.: subsidiary cells broad.

According to Tiffney (1977) the seed taxon *Magnolia burseracea* (Menzel) Mai is close to seeds which were described as *Magnolia waltonii* Tiffney from the Brandon lignite (Lower Miocene). From the carpologists point of view (Mai 1975, Tiffney 1977) neither of the two morphospecies is comparable to *Magnolia virginiana* L. Tiffney assumed *Magnolia schiedeana* Schlecht. as the nearest living descendant. But interestingly both *Magnolia virginiana* and *Magnolia schiedeana* have been assigned to a common clade (with the sections *Magnolia* and *Theorhodon*) of the molecular phylogenetic trees by Azuma et al. (2001). This clade belongs to the temperate disjunct groups, whose divergence time is assumed as late Eocene–Oligocene.

CLIMATE AND FACIES

The affinity of the *Magnolia* fossils of the Miocene seams in Lusatia to North American species *Magnolia virginiana* and *M. schiedeana* results in the integration into the temperate disjunct group according to Azuma et al. (2001). The delimitation from the tropical disjunct groups might also be facilitated by using epidermal characteristics. The investigated species *M. splendens* and *M. domingensis* are characterized by sunken stomata >35 µm in length (Fig. 6) and thick papillae.

The climatic indication of *Magnolia virginiana* and *M. schiedeana* in consideration of their distribution areas shows a large amplitude over twenty degrees in difference of latitude from temperate Massachusetts to Mexican tropical rainforest. On the other hand, in the humid belt along the east coast of North America with 1000–2000 mm precipitation, the areas are almost united, indicated by the "*Persea – Magnolia* – Moorwald" (Walter 1990).

Papilionaceophyllum liblarense respectively *Falcicutis varians* occur in the Lusatian Miocene almost exclusively within coal seams. In the 2nd Lusatian seam a normal succession proceeds according to the following stages (Schneider 1969, 2004): (1) swamp dominated by *Glyptostrobus europaeus* (Brongniart) Unger; (2) "hammocks" with *Sequoia abietina* (Brongniart) Knobloch; (3) Angiosperm – facies with *Papilionaceophyllum liblarense* Kräusel & Weyland, *Carpolithes burseraceus* Menzel, *Kalmiophyllum marcodurense* Kräusel & Weyland (Ericaceae), *Quercus rhenana* (Kräusel & Weyland) Knobloch & Kvaček, sabaloid palms, *Taiwania schaeferi* Schloemer-Jäger, and shoots from *Pinus*; (4) Glumiflore – reed; (5) *Pinus* – bog; (6) "*Marcoduria*" – facies (peat consisting of roots of conifers, probably *Cryptomeria, Cathaya* and *Sciadopitys*). The remains belonging to *Magnolia* are restricted to the Angiosperm – facies. In addition some *Falcicutis varians* occur in preparations of the *Sequoia* – and *Pinus* – facies. In general, the frequency of *Falcicutis* decreases with increasing importance of ombrotrophic conditions (presence of raised bogs).

Assuming a taxonomic connection between *Magnolia* – remains described from the 2nd Lusatian seam with the living species *M. virginiana* and *M. schiedeana* the habitats of this species will be described as follows. Tobe (1998) distinguished the evergreen *Magnolia virginiana* var. *australis* from the deciduous or partially evergreen *M. virginiana* var. *virginiana*. The first variety grows along the Gulf Coast, the latter on the Atlantic Coastal Plain. A typical habitat is the hardwood swamp in Florida. Monk (1966) proves a succession of three types of swamps: (1) cypress swamps with *Taxodium*; (2) deciduous hardwood swamps with *Sabal palmetto*, *Fraxinus caroliniana*, and *Ulmus floridana*; (3) evergreen hardwood swamps ("bayheads"). In the bayheads *Magnolia virginiana* grows in association with *Gordonia lasianthus* and *Persea palustris.* The understory may be characterized by *Myrica cerifera*, *Leucothoe* sp., and *Lyonia lucida*. The bayheads are seasonally flooded and form peat. The association with *Magnolia* represents the final stage of peat accumulation characterized by low values for cations and pH values (Monk 1966).

Additionally the "*Magnolia* Bogs" of the Washington D.C. area are of interest (Simmons & Strong 2003). Numerous small hanging bogs on the "Fall Line" dividing the Coastal Plain and Piedmont provinces are characterized by dominating *Magnolia virginiana* in a *Sphagnum* bog with monocotyledons (*Rhynchospora*, *Carex*, *Xyris*) and *Ilex laevigata*. The habitats of *Magnolia schiedeana* are "highly mixed tropical forests dominated by pines and oaks on mountain slopes with clay soils volcanically derived, elevated about 4000 feet" (comment on herbarium sheet Bot. Mus. Berlin).

STRATIGRAPHIC OCCURRENCE

The affinity of *Magnolia* remains to telmatic (peat-forming) habitats of the Paleogene and Neogene is evident. Hunger (1939) described one leaf determined as *Magnolia primigenia* Ung. from the Upper Eocene main seam of the Wählitz mine (Weißelster Basin, south-west of Leipzig). The leaf size comes to 25 × 5 cm. The cuticle is well preserved. Characteristics of stomata and trichome bases correspond to *Falcicutis varians* and *Papilionaceophyllum liblarense* respectively. These taphocoenoses consist predominantly of twigs and cones of *Quasisequoia couttsiae* (Heer) Kunzmann, needle-coals with *Pinus* sp. and leaves of Lauraceae. Moreover, in the Upper Eocene seam of the Etzdorf mine west of Halle dispersed cuticles showing the character of *Falcicutis varians* were found (Pl. 1, fig. 8). A dominant position of *Magnolia* as in the Miocene coals may be excluded for Paleogene mires. Likewise, the substitution of a large-leaved *Magnolia* by a microphyllous species together with an increasing frequency in the mire habitats of the Oligocene times, is significant.

In the Calau seam (Paleogene, Lower Oli-

Table 1. Frequency of *cuticulae dispersae Falcicutis varians* and *Kalmiophyllum marcodurense* in the Lusatian seam horizons 1 – 4. The mode of investigation (sampling, preparation, counting of cuticulae dispersae) for all seam horizons are identical

Seam horizon	Seam profiles investigated	*Falcicutis varians*		*Kalmiophyllum marcodurense*	
		Profiles with *Falcicutis* record	Profiles without *Falcicutis* record	Profiles with *Kalmiophyllum* record	Profiles without *Kalmiophyllum* record
1st Middle Miocene	15	11	4	8	7
2nd Middle+Lower Miocene	547	547	0	547	0
3rd Lower Miocene	27	5	22	12	15
4th Lower Miocene	105	21	84	59	46

gocene) of Lower Lusatia *Falcicutis varians* occurs for the first time together with *Kalmiophyllum marcodurense* Kräusel & Weyland (Ericaceae). Both species represent the most frequent dicotyledoneous plants in the mires in the Lusatian region in an interval from the Oligocene/Miocene boundary to the end of the Middle Miocene, independent of the absolute frequency in the different seam horizons. Table 1 indicates a striking change in the peat-forming conditions in the interval between the 3rd and 2nd seam horizon corresponding to the level of the Hemmoor transgression. This change does not concern the composition of the peat-forming association of angiosperms. On the other hand, the increasing frequency of cuticles in the 2nd seam horizon results from increasing degradation of tissues.

A corresponding stratigraphic distribution (Upper Oligocene to Upper Miocene) as for the leaf remains was found for *Carpolithus burseraceus* Menzel (Mai 1999b).

Comparing the Miocene seams of Lusatia with the main seam of the Lower Rhine region the composition of the seam-forming taphocoenoses is very similar. According to Kilpper (1960) the following "Standardvegetation" applies to the main seam in the Ville region: *Pinus* sp., Cyperaceae, (Poaceae), *Dioscoreophyllum liblarense* Kräusel & Weyland + further monocotyledons, *Forestiera petzoldii* Jähnichen & Walther, *Myrica integerrima* Kräusel & Weyland, *Papilionaceophyllum liblarense* Kräusel & Weyland, and *Kalmiophyllum marcodurense* Kräusel & Weyland.

CONCLUSIONS

The common occurrence of *Magnolia* fossils from different organs within an autochthonous taphocoenosis elucidates the difficulty of taxonomy in palaeobotanic research. This results from the specifications of the object under investigation reflected in the nomenclatural types. The botanist classifies whole plants, whereas the palaeobotanist is confronted with fossil leaves, dispersed cuticles, wood fragments, flowers, sporomorphs, seeds and fruits. The rules of botanical nomenclature do not sufficiently consider this fact. Special problems are typification, hierarchy, priority, use of generic names in palaeobotany, procedure in nomenclature of whole plant as result of synthesis, etc. The described fossils belonging to *Magnolia* are exemplary for palaeobotany.

The comparative research in peat-forming associations with *Magnolia* yield an arrangement symmetrical to both sides of the North Atlantic which originated from temperate disjunct groups, whose divergence time is assumed as late Eocene – Oligocene (Azuma et al. 2001). The following evolution on both sides of the Atlantic shows remarkable analogies in numerous characteristics such as leaf size and morphology, epidermal anatomy, seed size and morphology, habitat, and association with other peat-forming evergreen dicotyledons. The atlantic symmetry was disturbed in Europe only by the Ice Age.

ACKNOWLEDGEMENTS

I would like to express my gratitude to Dr. J. Van der Burgh (Universiteit Utrecht) for support in reading of particular papers; Prof. Dr. D.H. Mai (Humboldt-Universität Berlin), Prof. Dr. H. Walther, Dr. L. Kunzmann, (Museum for Mineralogy and Geology of the State Natural History Collections Dresden), and Dr. R. Vogt (Botanic Museum Berlin-Dahlem) for discussions and the possibility to use collections. I also would like to thank the reviewers for critical and careful examination of the manuscript.

Thanks are also due to Dipl.-Geol. R. Bönisch (Vattenfall Europe Mining, Cottbus) for joint fieldwork and sampling, Mrs. Dipl.-Geol. C. Niemz and Geol.-Ing. M. Meusel (LAOP Lauta) for support in micro-

scopy and preparation and Mr. R. Bowness Smith (Berlin) for linguistic correction of the manuscript.

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PLATES

Plate 1

Falcicutis varians Schneider (*cuticulae dispersae* belonging to *Papilionaceophyllum liblarense* Kräusel & Weyland)

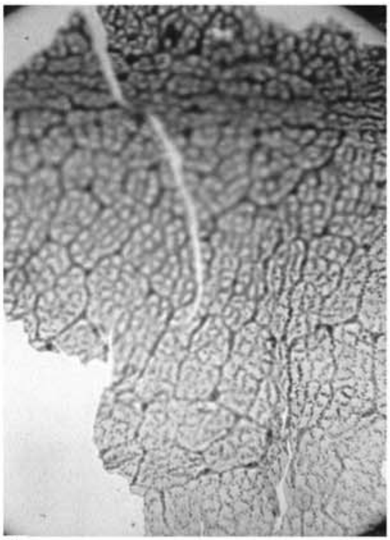
1. Adaxial cuticle. Hypodermis. Large outline of about hexagonal cells. 2nd Lusatian seam, Nochten mine, NQ 9820, prep. 4702
2. Adaxial cuticle. Internal secretory bodies as orginator of cuticle perforations. Anticlinal walls undulate with drop-shaped thickenings. Nochten mine, NQ 9820, prep. 4702
3. Abaxial cuticle. Stomata, trichomes, granular aggregates of epicuticular wax (**w**). 2nd Lusatian seam, Nochten mine, NQ 9635, prep. 3398
4. Abaxial cuticle. Immature stomatal complex. Guard mother cell (**m**) surrounded by lateral subsidiary cells (**s**) and encircling cells (**e**). Anticlinal cell walls with tendency to undulations indicated by drop-shaped thickenings. 2nd Lusatian seam, Nochten mine, NQ 9637, prep. 4270
5. Abaxial cuticle. "Twin stomata". Stomatal slits nearly invisible. Guard cell cuticle (**g**) very thin (white). Cuticle of the subsidiary cells (**s**) forms a narrow ring around the guard cells. Distal wall of subsidiary cells thick (see fig. 6). 1st Lusatian seam, Welzow mine, prep. 1783
6. Abaxial cuticle. Stoma surrounded by trichomes. Trichome base 1-celled (above) or 2-celled (on the left). Trichome cell (**t1**) partly turned down (below and on the right). 1st Lusatian seam, Welzow mine, prep. 1783
7. Abaxial cuticle. Outer layer of cuticle (cuticle in strict sense, thin) bearing the thick walled basal cells of the trichomes (**t1**). The cuticular layers are preserved only on a small area. They show outlines of epidermal cells, stomata and trichome bases. Seam "Piskowitz" (Miocene), Wetro mine (Upper Lusatia), prep. 2856

Falcicutis varians Schneider morphospecies

8. Abaxial cuticle with stomata. One stoma unfinished (**m**). Main seam (Upper Eocene), Etzdorf mine near Halle, prep. 431

Papilionaceophyllum liblarense Kräusel & Weyland

9. Transverse section of leaf in coal under reflecting light using fluorescence condition. Abaxial cuticle (**cab**) with trichomes (**t1**). Because of wax layer the abaxial cuticle appears thicker than adaxial cuticle (**cad**). Internal secretory bodies like cuticle of intense (yellow) fluorescence. 2nd Miocene seam (middle layer) of Lower Lusatia from Welzow, borehole no. 8424, sample no. 1.10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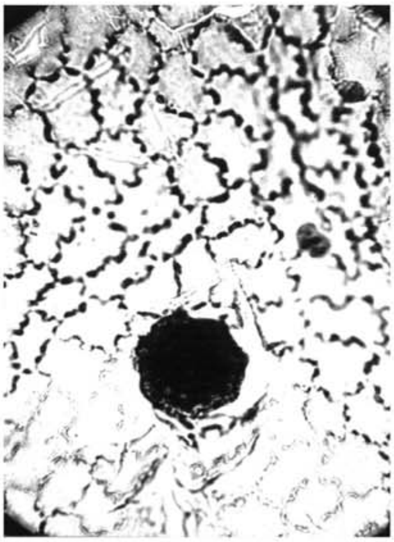
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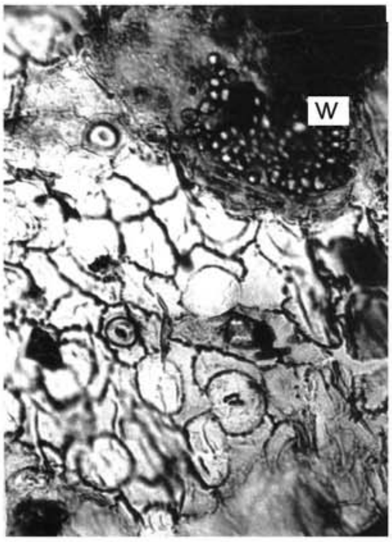
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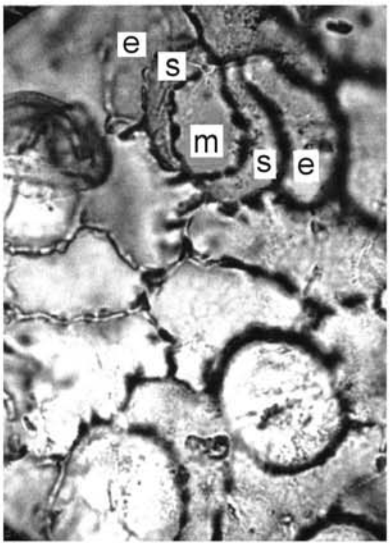
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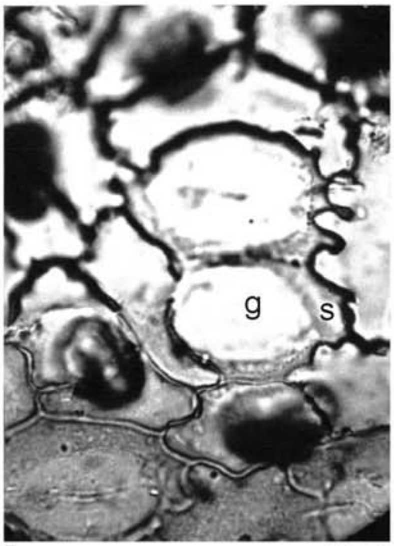
g
s
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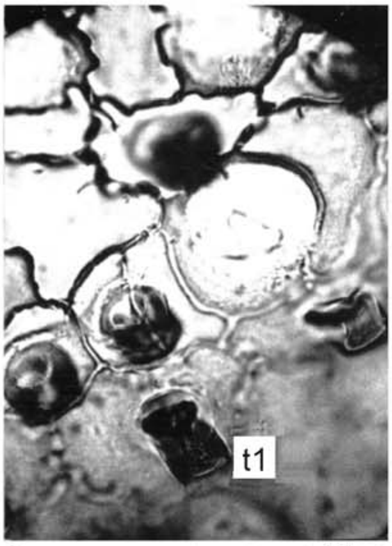
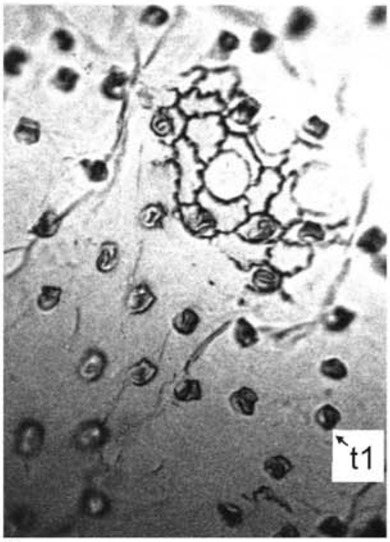
5


t1
20 µm

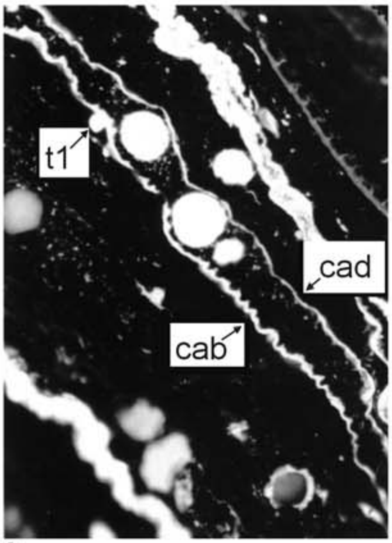
6


t1
50 µm

7


m
20 µm

8


t1
cad
cab
50µm

9

Plate 2

Papilionaceophyllum liblarense Kräusel & Weyland

1. Macroscopic view of taphocoenosis Nochten NQ 96 including numerous leaves. White leaves: abaxial surface covered by epicuticular wax. 2nd Lusatian seam, Nochten mine, NQ 9656
2. Detail of a leaf near the midvein (**mv**). Coalified leaf substance is partly broken off and splitted in the level of the mesophyll. The adaxial surface (**ad**) shows humps caused by secretory bodies. The abaxial epidermis (**ab**) is visible from the underside. 2nd Lusatian seam, NQ 9660

Carpolithus burseraceus Menzel

3. Detail of seed testa. Sclerotesta (**sct**) covered by relics of the sarcotesta (**sat**) consisting of densely arranged secretory bodies. 2nd Lusatian seam, Nochten mine, NQ 9826

Magnolia virginiana L.

4. Abaxial cuticle showing stomata and trichome (**t**), Hort. Botan. Tharandt. (Saxony). Prep. L 603

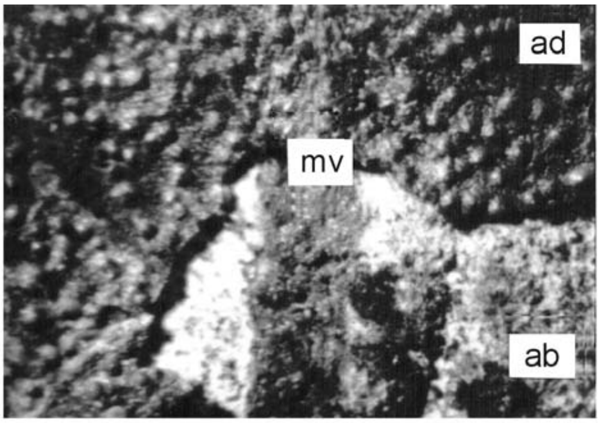
Magnolia schiedeana Schlecht.

5. Abaxial cuticle showing stomata and trichomes (**t**). Herb. Botan. Inst. Berlin-Dahlem. Prep. L 752

Magnolia splendens Urb.

6. Abaxial cuticle showing sunken stomata (**s**) and numerous trichomes (**t**). Herb. Botan. Inst. Berlin-Dahlem. Prep. L 754

1



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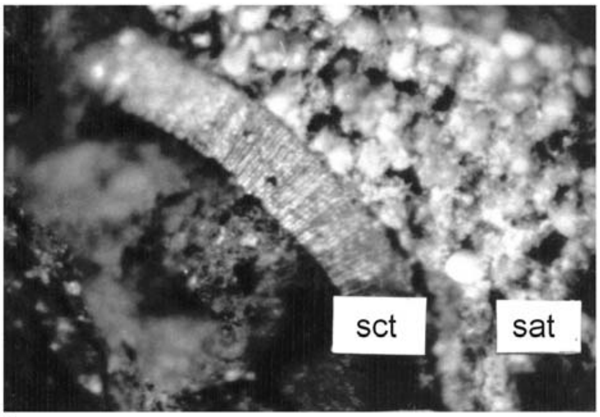

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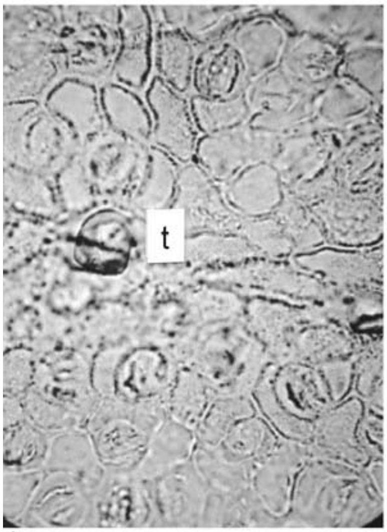

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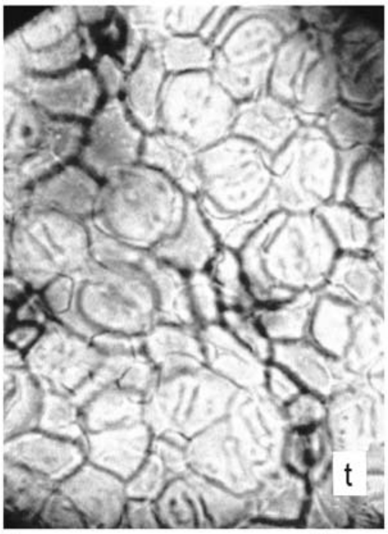

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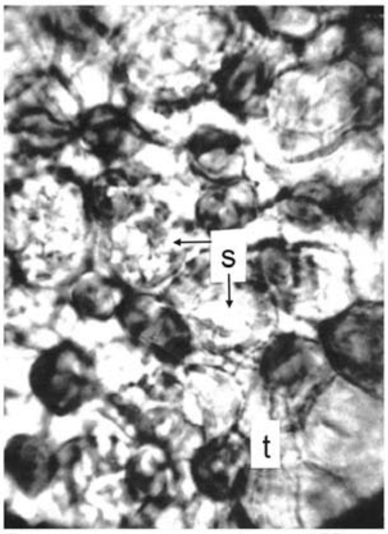

6