

# The flora of Mataschen – a unique plant assemblage from the late Miocene of eastern Styria (Austria)

JOHANNA KOVAR-EDER<sup>1</sup> and LILLA HABLY<sup>2</sup>

<sup>1</sup> Staatliches Museum für Naturkunde Stuttgart, Rosenstein 1, D-70191 Stuttgart, Germany;  
e-mail: eder.smns@naturkundemuseum-bw.de

<sup>2</sup> Botanical Department, Hungarian Natural History Museum Budapest, Pf. 222, H-1476 Hungary;  
e-mail: hably@bot.nhmus.hu

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**ABSTRACT.** A late Miocene (early Pannonian) leaf assemblage from the clay pit Mataschen, eastern Styria, Austria, is analysed. Thirty-eight species were determined, most of them by cuticular analysis. Among azonal taxa, only *Myrica lignitum*, *Platanus leucophylla*, and *Ulmus carpinoides* are abundant, while *Glyptostrobus europaeus*, *Alnus*, *Acer tricuspidatum*, and *Nyssa* occur in single or few specimens only. Zonal species diversity is distinctly higher (27 taxa) than the diversity of azonal ones, and 60% of the zonal taxa were probably evergreen. Among them, *Gordonia emanuelii* Kovar-Eder sp. n., *Gordonia pannonica* Kovar-Eder sp. n., *Gordonia styriaca* Kovar-Eder sp. n., *Schima mataschensis* Kovar-Eder sp. n., *Dicotylophyllum uhudler* Kovar-Eder sp. n. (Ericaceae), and “*Quercus*” *rhenanasimilis* Kovar-Eder sp. n., are described for the first time. *Symplocos rara* Kovar-Eder sp. n. is introduced. *Oleinites* cf. *liguricus* and *Smilax* cf. *protolanceaefolia* are described from Austria for the first time.

Five species of Lauraceae, 4 Theaceae, 2 Hamamelidaceae (among these cf. *Distylium*), one of *Symplocos*, and *Trigonobalanopsis rhamnoides* indicate close relations of this oryctocoenosis to floras of the “Younger Mastixioid” type that flourished in large parts of Europe during the early to early middle Miocene. The peculiar mixture of evergreen and deciduous taxa furthermore indicates relations to late Miocene/early Pliocene floras of southern parts of Europe (Romania, northern Mediterranean). In comparison, the similarities to the rich late Miocene Central European plant record are rather poor.

Based on the floristic composition, the evergreen broad-leaved forests at their ecotone towards the mixed mesophytic forests of south-east Asia constitute the most closely related modern zonal vegetation type. They thrive under a warm and humid Cfa-climate with the MAT range of approximately 15 to 19°C, the MAP range of 1280–1950 mm, and no average temperature of the coldest month below 0°C, although occasional frosts are possible.

**KEY WORDS:** foliage, cuticles, flora, palaeoecology, palaeoclimate, Pannonian, Miocene, Mataschen, Styria, Austria

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## INTRODUCTION

Due to favourable sedimentation conditions during the middle and late Miocene, the Central Paratethys region is very rich in fossil plant sites from the molasse basin north of the Alps eastwards to the Vienna, Styrian, and Pannonian Basins. Numerous floras have already been investigated, the most important and diverse being in Vösendorf and Laaergberg, Vienna (Berger 1952, 1955 a, b), the Hausruck-Kobernaussen region (Kovar-Eder 1988, Kovar-Eder & Wójcicki 2001), as well as Wörth and Paldau in eastern Styria (Kovar-Eder & Krainer 1990, Krenn 1998). Many taphocoenoses share low species diversity and high proportions of azonal taxa, e.g. Reith in eastern Styria (Kovar-Eder & Krainer 1991), Höllgraben near Weiz, Styria (Kovar-Eder & Krainer 1988), and Dozmat, western Hungary (Hably & Kovar-Eder 1996). The plant assemblage recently described from Mataschen from the base of the outcrop is also characterized by extremely low diversity, and all leaf taxa are azonal ones, characteristic of swampy environments (Kovar-Eder 2004). Surprisingly, the macro-morphologically poorly preserved leaf oryctocoenosis from the top of this outcrop turned out to be more diverse and richer in presumably zonal taxa than any other fossil flora of this region. Only collecting – including tiny, macro-morphologically indeterminable leaf fragments – and cuticular analysis of these specimens enabled us to obtain the results presented here. This underlines the necessity of continuing the search for and thorough investigation of fossil plant sites.

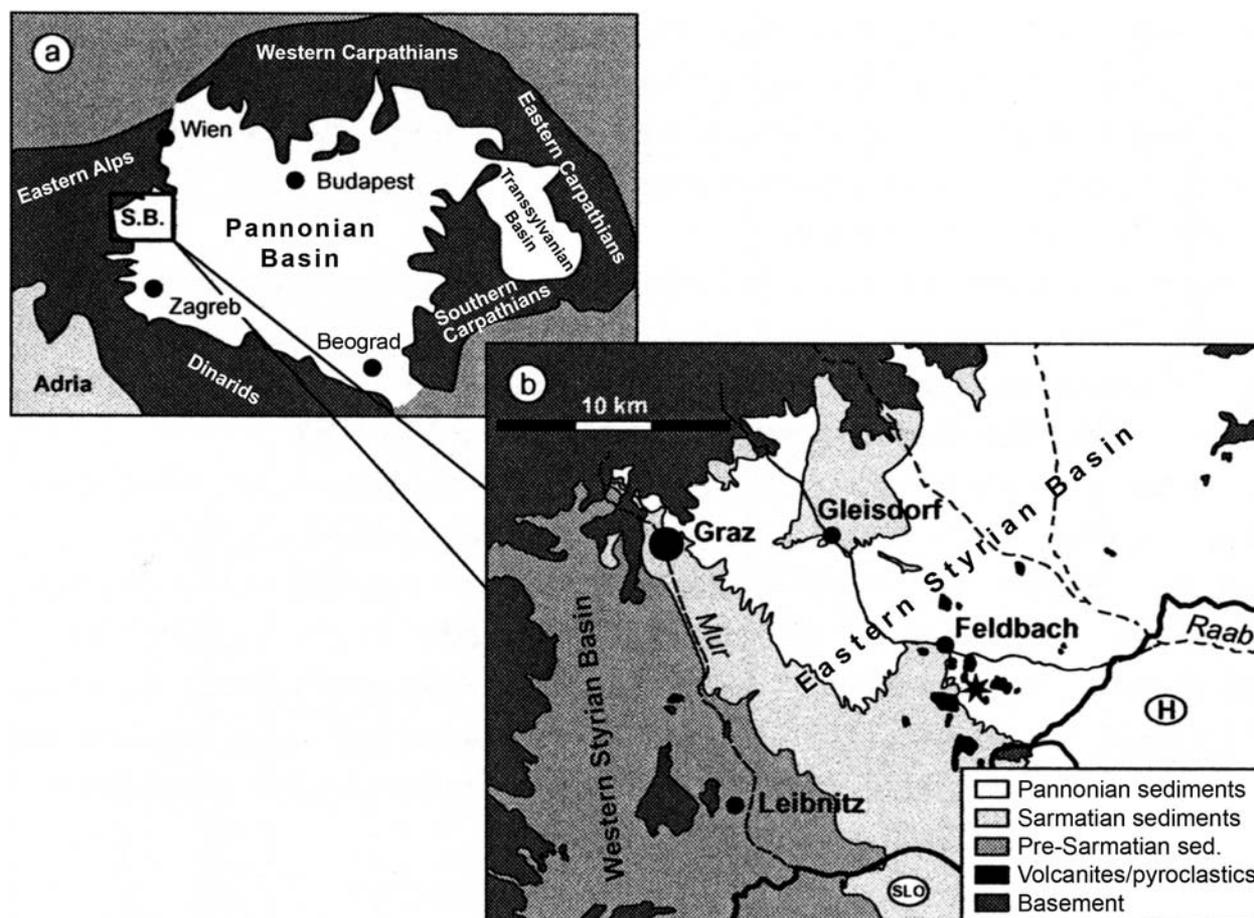
## GEOGRAPHICAL LOCATION, GEOLOGY, AND STRATIGRAPHIC CONTEXT

The clay pit Mataschen (“alte Grube”, 15°57'16"E/ 46°54'15"N) of the company Lias Austria GmbH (formerly Austrian Leca GmbH) is situated about 5 km SW of Fehring, district Feldbach, Styria (ÖK (Österreich Karte) 1: 50 000, sheet 192, Feldbach).

Geologically, Mataschen is situated in the Eastern Styrian Basin, which itself constitutes the westernmost extension of the Pannonian Basin (Fig. 1). About 30 m of sediments are exposed in the clay pit Mataschen (Figs 2, 3). The lowermost part is assigned to the Gleisdorf Formation. This is followed by clastic deposits of the Feldbach Formation, which itself is subdivided into the Eisengraben Member and the superimposed Sieglegg Member (Gross 2004a). Due to the rather high diversity of fossil organisms in the lacustric/fluviatile sediments of the Eisengraben Member, including calcareous nannoplankton, ostracods, molluscs, reptiles, fish, small mammals, plant remains (tree stumps in situ, leaves, fruits, pollen), this part of the section was already the subject of interdisciplinary research (Ćorić & Gross 2004, Daxner-Höck 2004, Gross 2004a, b, Harzhauser 2004, Kovar-Eder 2004, Meller & Hofmann 2004, Schultz 2004, Tempfer 2004). The correlation of these sediments with the *Mytilopsis ornithopsis*-zone (Pannonian, “zone” B sensu Papp 1951) is based on the occurrence of the bivalve *Mytilopsis ornithopsis* (Brusina 1892 in Harzhauser 2004). The superimposed silts and fine sands

of the Sielegg Member are characterized by a coarsening-upwards trend. These sediments yield pollen and, to a lesser extent, also fruits and seeds (Meller & Hofmann 2004); the uppermost part contains a leaf assemblage, which is subject of this paper. In the profile presented by Meller & Hofmann (2004: fig. 1) and refigured here (Fig. 3), this leaf assemblage derives from the interval 25–26.5 m,

*strobos* cones, wood fragments), and single fish scales, (coll. file no 2000B0015); 20–40 cm grey to brownish fine to middle-grained sands; 20–30 cm compact silt, at its base including a thin layer rich in plant remains (leaves, detritus, wood fragments; coll. file no 1998B0014) and in the higher parts with occasional carbonized leaf fragments only. Coll. file no. 2001B0012 was sampled directly above this 20–30 cm



**Fig. 1.** The Styrian Basin (S.B.) at the western margin of the Pannonian Basin during the Pannonian, **a** – overview of the Pannonian region, **b** – zoom in, after Gross (2004a, Fig. 2 modified)

from which the pollen sample P21 and the fruit sample D12 were investigated by Meller & Hofmann (2004). This interval (25–26.5 m) can be further subdivided as follows (from bottom to top): 60–70 cm silty, clayey, well-bedded, brownish sediment with abundant carbonized plant remains, especially numerous in the upper part (mainly leaf fragments but also bud scales, some fruits, exceptionally *Glypto-*

thick compact silt. The plant remains of this sample are already oxidized. The coarse, cross-bedded limonitic sands in the uppermost part of the exposure represent the Paldau Formation (Gross 2004a). The hanging wall of the exposure in Mataschen is a sliding area and the plant-bearing layers are strongly affected by ruptures.

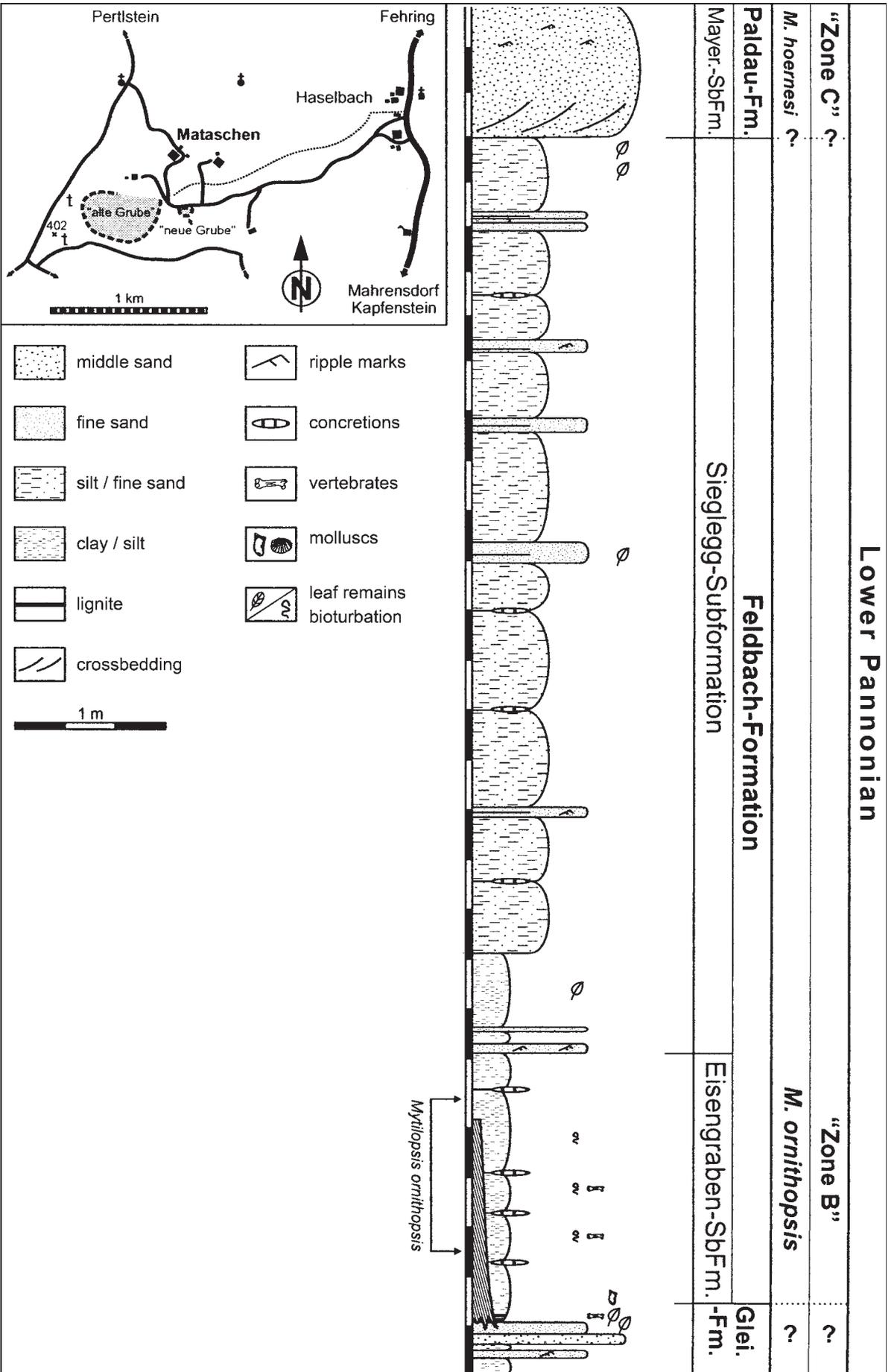


Fig. 2. Location of the site Mataschen and the profile at the outcrop, after Gross (2004a, Fig. 3 modified); at the base of the outcrop, in the level of the Eisengraben subformation in situ tree trunks are indicated

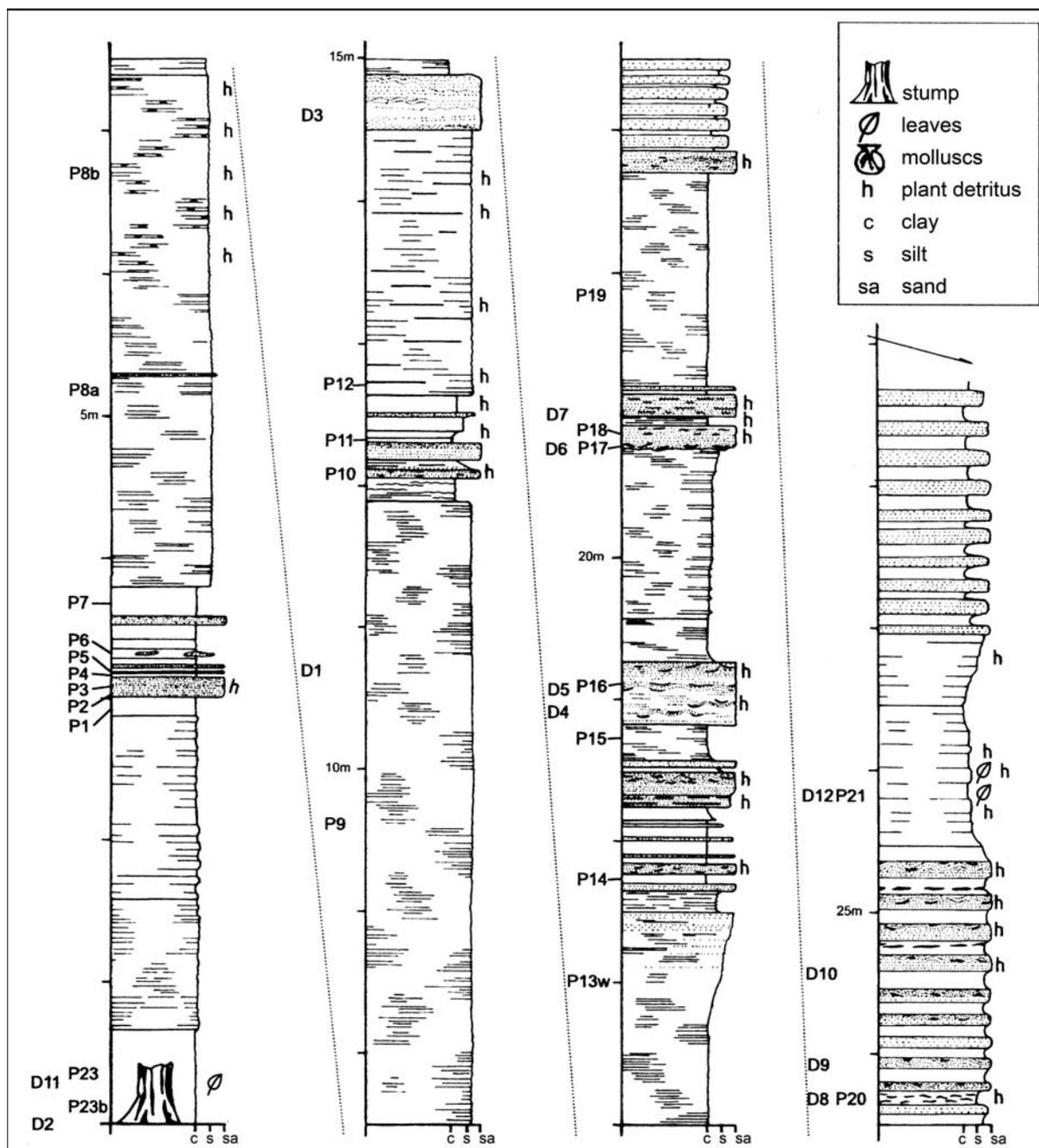


Fig. 3. Section at Mataschen "Alte Grube" from Meller & Hofmann (2004, fig. 1, modified) showing the exact locations of the basal and upper leaf-bearing sediments and the samples investigated for pollen and diaspores

## MATERIAL AND METHODS

The described fossil material was collected in excavation campaigns in 1995 and 1998. Due to fractioning of the sediment caused by sliding, no larger specimens were obtained. With few exceptions (coll. file no 1998B0014), the macro-morphological preservation of the carbonized plant remains is therefore rather poor. The plant-bearing layers were sampled. They yielded tiny blade fragments lacking almost any macro-morphological features (more than 550 specimens, Tab. 1), but the good cuticle preservation of many taxa enabled the description of this rich and exceptional flora. For

cuticular preparations, tiny carbonized fragments of the leaves were separated from the blades and the leaves then fixed with highly diluted cold-setting adhesive to avoid complete fragmentation and destruction due to drying.

In some species such as *Laurophyllum pseudoprinceps* and *Buxus pliocenica*, it was possible to separate the whole leaf from the sediment. These leaves were embedded on slides, a small amount of glycerol added, and then covered by a very thin plastic foil (food wrap).

Cuticles were prepared by the standard procedure with HCl (approx. 10%) followed by HF (approx.

10–20%) treatment, Schulze's reagents and KOH (5%). In many cases, the cuticles were already perfectly prepared after the treatment with Schulze's solution, so that KOH was not applied. The cuticles were usually stained with a safranin solution, but remained unstained when they were very delicate. The cuticles were embedded on slides fixed in glycerol and sealed with nail varnish.

For cuticle descriptions, representative values were obtained by measuring 3 leaves per taxon and taking 10 measurements of every cell type of these leaves. Minimum and maximum values are presented, and, in brackets, the minimal and maximal average values of the respective cell type of the measured leaves, e.g. stomatal length 15–30  $\mu\text{m}$  (20–27  $\mu\text{m}$ ). The terminology for the cuticular descriptions follows Dilcher (1974; stomatal complexes) and Metcalfe and Chalk (1979; trichomes). We follow the systematics of Judd et al. (1999).

Due to different usages of question marks and abbreviations such as cf. in the botanical/palaeobotanical literature, their usage here is defined as follows:

cf. in front of the generic epitheton refers to the genus, in front of the specific epitheton refers to the species.

The material is stored in the palaeobotanical collection of the Palaeontological Department of the Natural History Museum Vienna under the coll. file nos 1998B0014/, 2000B0015/, 2001B0012/.

Institutional abbreviations used in the text: NHMW – Natural History Museum Vienna, PRC – Prague Charles University, Faculty of Science.

## SYSTEMATIC PART

### CUPRESSACEAE

#### *Glyptostrobus europaeus* (Brongniart)

Unger

Pl. 1, fig. 1

1833 *Taxodium europaeum* Brongniart, p. 168.

1850a *Glyptostrobus europaeus* (Brongniart) comb.n., Unger p. 434.

**Material.** Coll. file nos: 2000B0015/155, 161, 162, 208, 217, 311 C.

**Description.** Small branch fragments with cupressoid, spirally arranged needles.

**Remarks.** Twig fragments of the water pine are rather rare in this assemblage. The distinction between twig fragments of *Glyptostrobus europaeus* and *Quasisequoia couttsiae* (Heer) Kunzmann may be ambiguous. Available cone fragments of *Glyptostrobus* from the same layer, clearly indicate that these rather poor twig fragments belong to the waterpine.

*G. europaeus* is by far the most common conifer in the Pannonian of the Styrian and Pannonian basins.

### MAGNOLIACEAE

#### *Magnolia liblarensis* (Kräusel & Weyland)

Kvaček

Pl. 1, figs 7–8, Pl. 3, figs 8, 12–13

1959 *Papilionaceophyllum liblarensis* Kräusel & Weyland, p. 111, pl. 24 figs 37–41, pl. 25 figs 42–47, pl. 26 fig. 48, textfigs 10,11.

1978 *Magnolia liblarensis* (Kräusel et Weyland 1959) comb. n., Kvaček p. 172.

**Material.** Coll. file nos: 2000B0015/55, 151, 211, 233, 264, 321 A.

**Description.** Fragments of simple, entire-margined leaves; lamina elliptic to slightly ? obovate, most complete specimen (no. 55, Pl. 1, fig. 8) 82 mm long (completed at least 100 mm), width 27 mm; base acute; apex acuminate (only in no. 151 preserved), midvein straight; only specimen no. 321 A (Pl. 1, fig. 8) is showing further venation details: secondaries brochidodromous, arising in distances of 4 mm at the base and 11 mm in the middle of the lamina; intersecondaries developed when the distances between the secondaries are wide, tertiaries fine, not very distinct, (forked) percurrent, higher-order venation forming a finely reticulate, polygonal network.

Adaxial cuticle (Pl. 3, fig. 13): rather thin, glabrous; non-modified epidermal cells with curved, straight or narrow undulate (U-shaped) anticlines, size 13–26  $\mu\text{m}$  (20–24  $\mu\text{m}$ ); anticlines about 1  $\mu\text{m}$  thick; glabrous.

Abaxial cuticle Pl. 3, fig. 12): medium thick, stomatal complexes: densely spaced, brachy-paracytic; stomata oval to almost orbicular, hardly staining, 21–32  $\mu\text{m}$  (25–28  $\mu\text{m}$ ) long, 17–23  $\mu\text{m}$  (19–20  $\mu\text{m}$ ) wide, stomatal aperture only faintly traceable, epidermal walls of the guard cells distinct, but not thickened; non-modified epidermal cells with narrow undulate (U-shaped), curved or sometimes straight anticlines, size 19–33  $\mu\text{m}$  (25–29  $\mu\text{m}$ ); anticlines about 1  $\mu\text{m}$  thick; roundish to oval bases frequent upon veins and in intercostal areas, poral rim of the base thickened, outer diameter (i.e. porus and poral rim included) 12–26  $\mu\text{m}$  (16–18  $\mu\text{m}$ ); basal trichome fragments sometimes preserved; lense-shaped

secretory bodies abundant, 25–61  $\mu\text{m}$  (41–43  $\mu\text{m}$ ) in diameter.

**Remarks.** *Magnolia liblarensis* was recently reported from early and middle Miocene deposits of Central Europe, Oberdorf (Ottangian, Kovar-Eder & Meller 2001), Kamenný Újezd in southern Bohemia (Knobloch & Kvaček 1996), and Sopron-Piuszpuszta (Sarmatian, Erdei 1996). Late Miocene to early Pliocene records derive from southern Europe: Delureni (Romania, Pannonian; Kvaček 1978), Meleto (Valdarno, Italy, Fischer & Butzmann 2002), and from the Lower Rhine Basin (Hambach, Inden Series, van der Burgh 2001). However, this is the first record of *Magnolia liblarensis* from the numerous Pannonian plant assemblages available from the Styrian and Vienna basins as well as from the molasse zone north of the Alps.

The record of *Magnolia* in the fruit spectrum from Mataschen is very scarce (present only in one sample but not from the leaf-bearing level itself). In the pollen flora, *Magnolia* is not recorded (Meller & Hofmann 2004).

#### LAURACEAE

### *Daphnogene polymorpha* (A. Braun) Ettingshausen

Pl. 1, figs 3–6, Pl. 4, figs 1–4

1845 *Ceanothus polymorphus* Al. Braun, p. 171.

1851 *Daphnogene polymorpha* (Al. Braun) Ettingshausen, p. 16, pl. 2 figs 23–25.

**Material.** Coll. file nos: 1998B0014/628, 633, 634; 2000B0015/ 5, 8, 12, 26 B, 33 A, 37, 44 B, 49, 50, 52 A, 59, 62, 76, 78 B, 80, 107, 113 A, 126, 127, 128, 130, 136, 154, 158, 163 A, 175 D, 189, 191, 193, 200, 202, 205, 221, 223, 228, 229, 230, 238 D, 239 A, 245, 248, 258 A, 273, 276, 312 A, 314 A, 319 A, 330, 335, 338, 346, 347, 361, 363, 368, 369, 378 A, 394, 431, 434, 453, 455 C, 461 A, C, 502 B, 506, 509; 2001B0012/474.

**Description.** Lamina slightly ovate to elliptic, very variable in size, 30–70 mm (up to 90 mm when completed, no. 361) long, 15–45 mm wide, base obtuse to acute, apex acuminate (preserved only exceptionally), margin entire; basal secondaries suprabasal acrodromous, running up into the apical third of the lamina; secondaries brochidodromous running in wide curves towards the margin, tertiaries

(forked-) percurrent; petiole up to 16 mm long, no further details available.

**Adaxial cuticle** (Pl. 4, figs 2, 4): medium thick, well preserved; non-modified epidermal cells with straight, curved, wavy or undulate anticlines, size 12–32  $\mu\text{m}$  (16–24  $\mu\text{m}$ ); anticlines about 1–2  $\mu\text{m}$  thick; one-celled, well-cutinized, polygonal to roundish trichome bases rare or absent, 7–12  $\mu\text{m}$  (8–9  $\mu\text{m}$ ) in diameter, poral rim slightly thickened and intensively staining, trichomes not preserved.

**Abaxial cuticle** (Pl. 4, figs 1, 3): medium thick to thin, stomatal complexes paracytic, roundish to broadly oval and mostly asymmetric, the hardly staining subsidiary cells largely covering the stomata, stomatal complexes 13–24  $\mu\text{m}$  (17–18  $\mu\text{m}$ ) long, 12–24  $\mu\text{m}$  (16–19  $\mu\text{m}$ ) wide, stomatal aperture hardly traceable, narrow, spindle-shaped, 5–10  $\mu\text{m}$  (6–7  $\mu\text{m}$ ) long; non-modified epidermal cells with straight, curved, wavy or undulate anticlines, size 10–22  $\mu\text{m}$  (15–16  $\mu\text{m}$ ); anticlines distinct, slightly thinner than on the upper leaf surface; trichome bases as on the upper leaf surface, rare to very frequent upon veins and in intercostal areas, 7–12  $\mu\text{m}$  (8–10  $\mu\text{m}$ ) in diameter, radial walls of the trichome base cells well cutinized; trichomes not preserved; lense-shaped secretory bodies often preserved, 21–49  $\mu\text{m}$  (32–34  $\mu\text{m}$ ) in diameter.

**Remarks.** Leaves of *Daphnogene polymorpha*, which is common in early to middle Miocene floras, are among the most abundant species in Mataschen, whereas leaves of the late Miocene taxon *D. pannonica* Kvaček & Knobloch have not been detected. *D. pannonica* differs from *D. polymorpha* by the relatively smaller size of its blades and a more delicate abaxial cuticle (Kvaček et al. 2002). Contrary to most of the other taxa from Mataschen, *D. polymorpha* leaves are macro-morphologically rather well preserved.

### *Laurophyllum pseudoprinceps* Weyland & Kilpper

Pl. 1, figs 9–12, Pl. 3, fig. 9, Pl. 4, figs 5–8

1963 *Laurophyllum pseudoprinceps* Weyland & Kilpper, p. 100, Fig. 6, pl. 23, figs 14–19.

**Material.** Coll. file nos: 1998B0014/623, 624; 2000B0015/38, 121, 135 A, 139, 219, 317, 321 B, 328 A, 348, 418, 420 A, 523–526, 528, 531, 533, 537, 539, 540, 541, 542, 545, 581, 583, 584, 611, 616, 617.

**Description.** Simple entire-margined leaves, shape (narrow) elliptic, base acute to obtuse, apex acute/acuminate, up to 65 mm (completed at least up to 80 mm) long, up to 40 mm wide; midvein straight or curved, secondaries brochidodromous, arising in distances of 5–11 mm, adjacent secondaries forming marginal loops; intersecondaries developed when secondaries are wider spaced; tertiaries and fourth-order veins forming each a distinct polygonal network, fifth-order veins forming rather quadrangular areoles? lacking free-ending veinlets.

Adaxial cuticle (Pl. 4, figs 6, 8): medium thick to thick, glabrous; size of non-modified epidermal cells 18–50  $\mu\text{m}$  (30–36  $\mu\text{m}$ ), anticlines undulate (U-shaped), wavy, curved or rarely straight, 1–2  $\mu\text{m}$  thick, with characteristic nodule-like thickenings.

Abaxial cuticle (Pl. 4, figs 5, 7): rather thick, glabrous, stomatal complexes brachyparacytic of butterfly-like shape; guard cells sunken, partly overlapped by the lateral, intensively staining subsidiary cells, stomata 18–27  $\mu\text{m}$  (20–23  $\mu\text{m}$ ) long, 13–23  $\mu\text{m}$  (16–19  $\mu\text{m}$ ) wide, stomatal aperture spindle-shaped to slit-like, 6–13  $\mu\text{m}$  (8–10  $\mu\text{m}$ ) long, outer stomatal ledges of the guard cells prominently thickened; non-modified epidermal cells with undulate, wavy, curved or rarely straight anticlines, size 17–46  $\mu\text{m}$  (27–31  $\mu\text{m}$ ), up to 1  $\mu\text{m}$  thick; lense-shaped secretory bodies present.

**Remarks.** As the above-discussed *Daphnogene polymorpha*, *Laurophyllum pseudoprinceps* is a rather common species in this leaf assemblage. Its blades are exceptionally well preserved and easily separated from the sediment (Pl. 1, figs 9–12).

### *Laurophyllum pseudovillense* Kvaček

Pl. 5, figs 5–6

1971 *Laurophyllum pseudovillense* Kvaček, p. 62, Fig. 10, pl. 1, figs 1–3, pl. 11, figs 1–3.

**Material.** Coll. file no: 2000B0015/360.

**Description.** The apical fragment of an entire-margined leaf, 37 mm long (completed at least twice that long), 26 mm wide, apex acute, venation brochidodromous;

Adaxial cuticle: not preserved; Abaxial cuticle (Pl. 5, fig. 5): thin, stomatal complexes paracytic, subsidiary cells round, nearly completely overlapping the stomata; stomata 15–

20  $\mu\text{m}$  (16  $\mu\text{m}$ ) long, stomatal aperture a short but distinct slit; non-modified epidermal cells distinctly dome-shaped, anticlines hardly traceable; polygonal trichome bases girdled by seven or even more cells, upon veins frequent and in intercostal areas common, inner diameter (i.e. porus excluding the poral rim) 8–16  $\mu\text{m}$  (12  $\mu\text{m}$ ), commonly short, fragmentary trichome remains still adherent, all cell types almost homogeneously staining; isolated large lense-shaped secretory bodies preserved, 34–66  $\mu\text{m}$  (55  $\mu\text{m}$ ) in diameter.

**Remarks.** The type material of *Laurophyllum pseudovillense* (Kvaček 1971) from Hrádek nad Nisou, Bohemia (early/middle Miocene), has been studied for comparison (holotype figured here Pl. 5, fig. 6). In *L. pseudovillense* the adaxial cuticle is rather thick and usually preserved (with fairly constantly straight-walled anticlines of the non-modified epidermal cells), but in our specimen from Mataschen, we were unable to prepare the adaxial cuticle. Moreover, the trichome bases of the specimen described here still bear distinct remains of the trichome-foot, thus being somewhat different from *L. pseudovillense* from Hrádek and from Wackersdorf (Knobloch & Kvaček 1976). In the specimen from Mataschen, the non-modified epidermal cells on the abaxial cuticle are characteristically dome-shaped. Although this feature has not been described explicitly by Kvaček (1971), it is visible in the cuticle preparations from Hrádek and is shown in the drawing in text-fig. 10 there. *Laurophyllum pseudovillense* is generally a rare member of the fossil Lauraceae, and usually documented by single or few leaves only. So far, this taxon was known from late early to (early) middle Miocene localities only, e.g.: Wackersdorf, Germany, (Knobloch & Kvaček 1976) and Horní Bříza, Plzeň Basin, West Bohemia (Němejc et al. 2002).

### *Laurus abchasica* (Kolakovský & Shakryl) Ferguson

Pl. 1, fig. 2, Pl. 5, figs 1–4

1958 *Laurophyllum abchasicum* Kolakovský & Shakryl, in Kolakovský, p. 346, pl. 7 figs 1–3, pl. 10 figs 4–8.

1974 *Laurus abchasica* (Kolakovský & Shakryl) comb. n., Ferguson, p. 64, figs 7 A-H, 8 A-D, 9 A-D.

**Material.** Coll. file nos: 2000B0015/23, 27, 420 B, 343, 461, 502 C.

**Description.** Specimen no. 27 (Pl. 1, fig. 2) lamina of a large leaf lacking base and apex, 62 mm (up to 100 mm when completed) long, 50 mm wide, shape elliptic, margin entire, secondaries probably brochidodromous, arising in distances of 16–19 mm, running slightly curved towards the margin; tertiaries distinct, partly percurrent, fourth-order venation forming a polygonal network, enclosing the quadrangular to hexagonal fifth-order venation; specimen no. 502 C showing the acute leaf base; other fragments lacking diagnostic features.

Adaxial cuticle (Pl. 5, fig. 2): thick, glabrous, size of non-modified epidermal cells 19–45  $\mu\text{m}$  (29–35  $\mu\text{m}$ ), anticlines mostly U-shaped, rarely  $\Omega$ -shaped undulate, up to 1  $\mu\text{m}$  thick.

Abaxial cuticle (Pl. 5, figs 1, 3, 4): (medium) thick, stomatal complexes paracytic, shape rhomboidal, the well-staining subsidiary cells largely overlapping the sunken guard cells; guard cells less intensively staining, stomata 16–24  $\mu\text{m}$  (18–20  $\mu\text{m}$ ) long, stomatal aperture spindle-shaped to slit-like, 10–16  $\mu\text{m}$  (11–12  $\mu\text{m}$ ) long; size of non-modified epidermal cells 19–44  $\mu\text{m}$  (25–31  $\mu\text{m}$ ), anticlines undulate (usually narrower than on the adaxial cuticle), distinctly to hardly traceable, up to 1,5  $\mu\text{m}$  thick; occasionally one-celled, well cutinized, roundish trichome bases present in intercostal areas and upon veins, 7–13  $\mu\text{m}$  (10–11  $\mu\text{m}$ ) in diameter, radial walls of the trichome base cells sometimes more strongly cutinized; trichomes not preserved; lense-shaped secretory bodies present, 26–61  $\mu\text{m}$  (41–54  $\mu\text{m}$ ) in diameter.

**Remarks.** As in the foregoing taxon, leaves of *Laurus abchasica* are usually not abundant. Remarkably, six leaves could be assigned to this taxon based on cuticular structures. This laurel is well documented especially from the early and early middle Miocene of Central Europe: North and South Bohemia, e.g. Kvaček (1971), Bůžek et al. (1996), Knobloch & Kvaček (1996), Germany i.e. Wackersdorf region Knobloch & Kvaček (1976) and Kreuzau (Ferguson 1971, 1974), and Austria, Oberdorf, (Kovar-Eder & Meller 2001). Described as *Cornus graeffii*, *Laurus abchasica* was wrongly identified in the flora from Bergheim, Inden Formation (Upper Miocene), Lower Rhine Basin (Belz & Mosbrugger 1994). *Laurus abchasica* is also well known from the

classical late Miocene/Pliocene refuge regions in the Colchic region, e.g. Duab, Abchasia (Kolakovsky 1958), and the Balkan Peninsula, e.g. Valeă de Cris, Romania (Givulescu 1975). This is the first record of *L. abchasica* from the late Miocene of Central Europe.

### *Laurophyllum* sp.

Pl. 1, fig. 13, Pl. 5, figs 7–8

**Material.** Coll. file no: 2000B0015/6.

**Description.** A single fragment of the basal half of an ? elliptic blade, 30 mm long (about 60 mm when completed), 27 mm wide; base obtuse, petiole straight, slender, 7 mm long but incomplete; leaf margin entire; midvein straight, secondaries arising at 7–8 mm distances (3 preserved only), running slightly curved across the lamina, their marginal course not discernible.

Adaxial cuticle (Pl. 5, fig. 8): rather thin, glabrous, anticlines of the non-modified epidermal cells somewhat U-shaped, undulate and slightly irregularly thickened, size of non-modified epidermal cells 18–38  $\mu\text{m}$ .

Abaxial cuticle (Pl. 5, fig. 7): delicate, poorly preserved, glabrous; stomatal complexes not very distinct, brachyparacytic, butterfly-like in shape, 14–19  $\mu\text{m}$  long, aperture almost reaching the poles; outlines of the non-modified epidermal cells hard to trace, anticlines straight to slightly curved, size 14–23  $\mu\text{m}$ .

**Remarks.** This leaf remain certainly represents a further member of the Lauraceae in the flora of Mataschen. It might be mistaken for a poorly preserved specimen of *Laurophyllum pseudoprinceps*, but differs by its smaller stomata. However, the preservation hinders a more exact identification.

## BUXACEAE

### *Buxus pliocenica* Saporta & Marion

Pl. 1, figs 14–18, Pl. 3, fig. 10, Pl. 6, figs 1–2, Pl. 8, fig. 8

1876 *Buxus pliocaenica* Saporta et Marion, p.144, pl. 32 figs 6–8.

**Material.** Coll. file nos: 1998B0014/622, 638–649; 2000B0015/16A, 384, 527, 529, 530, 532, 534–536, 538, 543, 544, 546–550, 577–579, 585–590, 592, 593, 595, 597–608, 610, 613–615.

**Description.** Leaves (narrow) elliptic to slightly (narrow) ovate or obovate, more or less asymmetric, entire-margined, texture coriaceous, 10–31 mm long, 6–14 mm wide, base acute to obtuse, petiole short, 1–2 mm long, apex usually slightly emarginate, midvein straight, stout, secondaries very densely spaced, camptodromous, once to several times branched, bent upwards and running parallel with numerous intersecondaries towards the margin, forming there a well-developed fimbrial vein; higher order veins exmedially ramified, running parallel with the secondaries and intersecondaries, forming imperfect areoles.

Adaxial cuticle (Pl. 6, fig. 2): thick, glabrous; size of non-modified epidermal cells 23–37  $\mu\text{m}$  (29  $\mu\text{m}$ ), anticlines straight, about 2  $\mu\text{m}$  thick, forming 4- to 6-sided cells.

Abaxial cuticle (Pl. 6, fig. 1): thick, glabrous; stomatal complexes anomocytic, stomata large, rather round, subparallelly oriented, 28–38  $\mu\text{m}$  (33  $\mu\text{m}$ ) long, 29–40  $\mu\text{m}$  (33  $\mu\text{m}$ ) wide, stomatal aperture narrow spindle-shaped, 7–16  $\mu\text{m}$  (12  $\mu\text{m}$ ) long, polar T-pieces and a thick, well-developed circular cuticular ring surrounding the aperture; non-modified epidermal cells as on the adaxial side: size 22–37  $\mu\text{m}$  (29  $\mu\text{m}$ ), anticlines straight, about 2–3  $\mu\text{m}$  thick forming 4- to 6-sided cells.

**Remarks.** *Buxus pliocenica* is rather common in this assemblage. Its leaves are very well preserved and are among those few taxa whose blades are easily separated from the sediment and transferred to slides. Some Badenian and Sarmatian records of *Buxus* formerly assigned to *B. pliocenica* – from Smolkov near Opava, Moravia (Knobloch 1969), Türkenschanze, Vienna Basin (Berger & Zabusch 1953) – were reidentified by Kvaček et al. (1982) as probably representing *Buxus egeriana* Kvaček, Bůžek & Holý.

*Buxus* is also documented in pollen sample P21 from the leaf-bearing layer (Meller & Hofmann 2004).

#### PLATANACEAE

##### *Platanus leucophylla* (Unger) Knobloch

Pl. 2, figs 1–4, Pl. 6, figs 3–6

1850b *Populus leucophylla* Unger, p. 417.

1971 *Platanus leucophylla* (Unger) comb. n., Knobloch, p. 263.

**Material.** Coll. file nos: 2000B0015/10 B, 29,

32, 40, 54, 63, 65, 67 A ?, 93 A, 117 A, 141, 142, 144 ?, 147 ?, 148 A, 169, 235 B, 238 A, 240 A, 257, 280 A, B, 285, 288 A, 296 B, 322 A, 355 B ?, 356 ?, 384, 390 B, 404, 411, 421, 422 A ?, 447 ?, 448 B ?, 451, 454, 456, 511, 513 B ?.

**Description.** Only few specimens largely complete; petiole up to 17 mm long (incomplete), straight and stout, lamina palmate, three-lobed, central lobe 90 mm long (complete in no. 117 A, Pl. 2, fig. 3), in no. 54 85 mm long, but incomplete (at least 100 mm when completed), from apex to apex of the lateral lobes at least up to 120 mm wide; base acute, apices of lobes acute/acuminate, margin with distinct hook-like teeth, basal side of teeth convex (straight), apical side concave (straight), base rounded, apex acute, main veins stout, venation palinactinodromous, originating suprabasally acrodromous (in no. 32 exceptionally basally acrodromous), ending in the apices of the lobes; simple craspedodromous secondaries arise from the main veins, they fork occasionally and end in marginal tooth apices; tertiaries forked – percurrent; further venation details not preserved.

Adaxial cuticle (Pl. 6, figs 4, 6): medium thick, glabrous, faint parallel cuticular striation along veins; size of non-modified epidermal cells 22–59  $\mu\text{m}$  (31–42  $\mu\text{m}$ ), anticlines straight to curved, 2–4  $\mu\text{m}$  thick.

Abaxial cuticle (Pl. 6, figs 3, 5): rather thin, with distinct cuticular striation running parallel on the elongated cell outlines above veins, radially orientated around stomata and trichome bases, and forming parallel, wavy bundles upon the non-modified epidermal cells; stomatal complexes cyclocytic, a very narrow but well-distinguishable ring surrounding the stomata, stomata 24–46  $\mu\text{m}$  (31–38  $\mu\text{m}$ ) long, 19–37  $\mu\text{m}$  (25–30  $\mu\text{m}$ ) wide, stomatal aperture oval, 12–29  $\mu\text{m}$  (19–23  $\mu\text{m}$ ) long, poral and epidermal walls of the guard cells distinct but unthickened, slender polar I-pieces developed; non-modified epidermal cells with straight to curved anticlines, size 18–49  $\mu\text{m}$  (27–34  $\mu\text{m}$ ); anticlines about 2  $\mu\text{m}$  thick; upon veins and in intercostal areas occasionally large, roundish to polygonal, four- to five-celled trichome bases, 13–31  $\mu\text{m}$  (21–25  $\mu\text{m}$ ) in diameter, poral wall of the trichome base cells slightly thickened, trichome pore forming marginally the radial walls of the trichome base cells, occasionally fragments of the trichome foot preserved.

**Remarks.** Specimen no. 32 lacks the characteristic platanoid shape because marginal teeth are scarce and tiny, and the main veins originate directly at the base (basally acrodromous). However, the cuticle is characteristic of *Platanus leucophylla*.

Although this species is documented in Central Europe since the Badenian, and is richly available from the late Miocene, cuticle descriptions are rare (Ferguson 1971, Belz & Mosbrugger 1994). In all these cases, the stomata are also surrounded by a narrow ring (Ferguson 1971, Belz & Mosbrugger 1994), indicating the cyclocytic type of stomatal complexes. Unfigured and lacking description, *Platanus leucophylla* has been listed by Mai & Walther (1991) for floras assigned to the "Brandis floral complex", which the authors assign to the early Miocene. We regard these records as being somewhat ambiguous.

The pollen spectrum from the leaf-bearing level includes also *Platanus*, while most of the samples from the section below lack it (Meller & Hofmann 2004).

#### HAMAMELIDACEAE

##### cf. *Distylium heinickei* Walther

Pl. 1, fig. 20, Pl. 7, figs 1–3

1991 cf. *Distylium heinickei* Walther n. spec., Mai & Walther, p. 46, pl. 25 figs 1–4, Fig. 6:1–3.

**Material.** Coll. file nos: 2000B0015/72A, 339A, 409.

**Description.** Three fragments available, only no. 72A (Pl. 1, fig. 20) with some macro-morphological details: basal part of a relatively thin leaf, 29 mm long (incomplete), 22 mm wide; lamina split into tiny fragments, the probably entire leaf margin is shiny skin-like and brownish; two secondaries arising in 10 mm distance, slender, running in a wide curve across the lamina.

Adaxial cuticle (Pl. 7, fig. 2): medium thick, glabrous; size of non-modified epidermal cells 27–62  $\mu\text{m}$  (38–48  $\mu\text{m}$ ), anticlines U-shaped undulate or rarely curved, 1–3  $\mu\text{m}$  thick.

Abaxial cuticle (Pl. 7, figs 1, 3): thick, well preserved, smooth, glabrous; stomatal complexes brachyparacytic with lateral, rather narrow, often sculptured subsidiary cells; stomata (broad) oval, 18–26  $\mu\text{m}$  (22–23  $\mu\text{m}$ ) long, 15–21  $\mu\text{m}$  (18–19  $\mu\text{m}$ ) wide, cuticle above

guard cells rather thick, epidermal walls of the guard cells and outer stomatal ledges of the guard cells thickened, outer front cavity oval to roundish, 8–15  $\mu\text{m}$  (11–13  $\mu\text{m}$ ) long, polar I-shaped thickenings present; size of non-modified epidermal cells 26–50  $\mu\text{m}$  (35–43  $\mu\text{m}$ ), U-shaped undulate, undulations deeper than on the adaxial cuticle; anticlines about 1  $\mu\text{m}$  thick; along veins, cuticular striation running parallelly to the elongated cell outlines.

**Remarks.** The cuticle of the here described fossils differ from *Distylium fergusonii* by the absence of the very characteristic trichome bases; however, a scattered presence of such trichome bases in the specimens from Mataschen cannot be excluded because the preserved cuticle fragments are rather tiny. Our material resembles *D. heinickei* Walther (Mai & Walther 1991), in which trichome bases are comparably scarce. We may, however, deal with a further, yet unknown species because *D. heinickei* has been reported so far only from the late Oligocene of Bockwitz and Kleinsaubernitz (*Distylium cf. heinickei*), while the here described leaves are of late Miocene age.

*Distylium* sp. from Weingraben (Burgenland, Austria, Badenian) also lacks trichome bases (Jechorek & Kovar-Eder 2004). The preserved cuticle fragments are even smaller than those from Mataschen, possibly therefore lacking trichome bases. In the specimen from Weingraben, the stomata are bigger than in those from Mataschen.

Among modern Hamamelidaceae the cuticles of *Sycopsis* and *Distylium* are very similar and their discrimination is problematic (Ferguson 1974, Knobloch & Kvaček 1976). Due to the rich fossil record of *Distylium* fruits in the European Neogene, such leaf remains are assigned to *Distylium*.

Neither the fruit nor the pollen record of Mataschen includes *Distylium*.

##### ? *Corylopsis* sp.

Pl. 1, fig. 21, Pl. 6, figs 7–8

**Material.** Coll. file no: 2000B0015/91.

**Description.** One fragmentary leaf, 26 mm long, 15 mm wide, base and apex not preserved, leaf margin fragmentarily and poorly preserved only, ? entire or ? toothed, secondaries arising regularly in distances of approximately 7–9 mm, running parallel towards the

margin, marginal course not visible, tertiaries distinctly simple percurrent.

Adaxial cuticle: not preserved.

Abaxial cuticle (Pl. 6, figs 7, 8): very delicate, preserved in small fragments only; type of stomatal complexes unclear, stomata roundish to oval, 18–23  $\mu\text{m}$  (20  $\mu\text{m}$ ) long, 15–20  $\mu\text{m}$  (18  $\mu\text{m}$ ) wide, epidermal walls of the guard cells faint, outer stomatal ledges of the guard cells well developed, front cavity oval, 8–11  $\mu\text{m}$  (9  $\mu\text{m}$ ) long, the stomatal aperture almost reaching the poles; anticlines of the non-modified epidermal cells not traceable; small, strongly cutinized cells form polygonal, prominent trichome bases, especially situated above veins, outer diameter 27–46  $\mu\text{m}$  (31  $\mu\text{m}$ ); trichomes not preserved.

**Remarks.** The density and almost parallel course of the secondary veins of this leaf fragment are reminiscent of Rhamnaceae, Cornaceae, and Hamamelidaceae (*Corylopsis/Parrotiopsis*). Unfortunately, the poorly preserved leaf margin is not suitable for a more precise identification and the cuticle is rather poorly preserved. However, the prominent multicellular trichome bases remind those of the Hamamelidaceae and exclude the Rhamnaceae (Jones & Dilcher 1980). Moreover, the brachyparacytic type of the stomatal complexes is characteristic of the Hamamelidaceae. There, in taxa with delicate cuticles, only the stomata may be visible, while the outlines of the subsidiary cells and the non-modified epidermal cells are poorly reflected on the cuticle.

The cuticle of *Parrotia pristina* (Ettingshausen) Stur is rarely preserved and has been described by Knobloch and Kvaček (1976). The anticlines of the subsidiaries as well as the straight to curved anticlines of the non-modified epidermal cells are developed on the cuticle; even more relevant for the distinction from the here described leaf, the stomata are larger (18–) 20–(30)  $\mu\text{m}$ .

Among the numerous representatives of different genera of the Hamamelidaceae in the collection of the PRC, one slide labelled as *Corylopsis wilsonii* Hemsl. (Steward & Cheno no. 967, San Chiang Hsien, Quangxi) shows a close resemblance in the small size and shape of the stomata as well as in the absence of anticlines in both the subsidiary cells and the non-modified cells. However, this cuticle

differs from the Mataschen specimen by the dome-shaped surface of the non-modified epidermal cells. Moreover, on the same slide, there is another fragment of the abaxial cuticle adjacent to a strong vein. On this cuticle fragment, the anticlines are well preserved, the non-modified cells and subsidiaries are well traceable, the non-modified ones are dome-shaped, and the stomata are distinctly larger than on the other cuticle fragment fixed on this slide. The discrepancy in stomatal size of the two cuticle fragments raised doubts as to whether these fragments belong to the same specimen and species. Not only for this reason, detailed studies of *Corylopsis* are necessary to clarify whether the here described specimen unambiguously represents this genus. Better preservation of the leaf margin of the specimen from Mataschen could support the identification as in *Corylopsis* the leaf margin is characteristically toothed. The documentation of *Corylopsis* foliage in the European Neogene would be remarkable because fruit records are available from many European sites (*Corylopsis urseleensis* Mädlér) and pollen have been reported so far, e.g. in Czarny Dunajec, Chyżne Lipnica Mała, Poland (Oszast & Stuchlik 1977) and in Bulgaria (Ivanov et al. 2002).

#### VISCACEAE

##### *Viscum morlotii* (Unger) Knobloch & Kvaček

Pl. 1, fig. 19, Pl. 7, figs 5–6

1850b *Potamogeton morlotii* Unger, p. 323.

1976 *Viscum morlotii* (Unger) comb. n., Knobloch & Kvaček, p. 67, pl. 12 fig. 17, pl. 17 figs 5, 13, pl. 33 figs 4–11.

**Material.** Coll. file nos: 1998B0014/630; 2000B0015/580, 618.

**Description.** Specimen no 630 (Pl. 1, fig. 19) is almost complete: lamina coriaceous, entire-margined, obovate, 29 mm long, 18 mm wide, base cuneate, apex probably rounded, petiole thick and stout, venation hardly visible.

Ab- and adaxial cuticles (Pl. 7, figs 5, 6): thick, amphistomatic; stomatal complexes brachyparacytic, wide oval, butterfly-like shape, subsidiary cells partly covering the guard cells; stomata 58–78  $\mu\text{m}$  (61–65  $\mu\text{m}$ ) long, stomatal aperture spindle-shaped, 31–48  $\mu\text{m}$  (35–40  $\mu\text{m}$ ) long; subsidiary cells occa-

sionally with faint striation perpendicular to the longitudinal axis of the guard cells; size of non-modified epidermal cells 40–113  $\mu\text{m}$  (50–82  $\mu\text{m}$ ), anticlines straight or rarely curved, 1–4  $\mu\text{m}$  thick, sometimes knob-like; polygonal openings (? hydathodes) with thickened margins occasionally present, diameter 47–67  $\mu\text{m}$  (59  $\mu\text{m}$ ; thickened poral rim excluded).

**Remarks.** This probably semi-parasitic species is a very common accessory element in the Neogene European floristic record. One further remain of *Viscum* is included in the fruit record. It derives from a layer below the upper leaf-bearing one (Meller & Hofmann 2004).

#### ROSACEAE

##### *Rosa* sp.

Pl. 1, fig. 22, Pl. 7, fig. 4

**Material.** Coll. file nos: 2000B0015/35, 135 B, 210.

**Description.** Probably leaflets, elliptic, 15–23 (when completed 17–25) mm long, 9–15 mm wide; base obtuse to acute, apex not preserved, margin serrate, teeth tiny and variable in shape; except for the midvein, no venation details preserved.

Adaxial cuticle: not preserved.

Abaxial cuticle (Pl. 7, fig. 4): delicate, poorly preserved, tiny fragments; type of stomata unclear, ? anomocytic, stomata quite variable in shape and size, roundish to oval, 12–26  $\mu\text{m}$  (17  $\mu\text{m}$ ) long, 11–18  $\mu\text{m}$  (15  $\mu\text{m}$ ) wide, stomatal aperture 6–15  $\mu\text{m}$  (9  $\mu\text{m}$ ) long; size of non-modified epidermal cells 15–26  $\mu\text{m}$  (19  $\mu\text{m}$ ), anticlines difficult to trace, probably curved to slightly wavy.

**Remarks.** Here, we summarize three fragments of probable leaflets. In specimen no. 210 the macro-morphology is best preserved (Pl. 1 fig. 22) but cuticle preparations were not successful. From nos 135 B and 210, tiny, delicate cuticle fragments have been prepared. We suppose that these remains belong to *Rosa*. Records of *Rosa* including their cuticles are rather rare, e.g. *Rosa lignitum* Heer, (synonym *R. bohemica* Engelhardt) Haselbach, Germany, early Oligocene (Mai & Walther 1978). *Rosa* has been determined based on a compound leaf and its cuticle from Kreuzau (Ferguson 1971) and *Rosa styriaca* Kovar-Eder has been

described from the early Pannonian of Höllgraben near Weiz, northwestern margin of the Eastern Styrian Basin (Kovar-Eder & Krainer 1988). We hesitate to assign the leaf fragments from Mataschen to this species because, there, the marginal serration is rather uniform. Generally, macro-morphology is more decisive for the identification of *Rosa* than the cuticle, the latter being rather uncharacteristic.

#### ULMACEAE

##### *Ulmus carpinooides* Göppert sensu Menzel

Pl. 1, figs 23–26

1855 *Ulmus carpinooides* Göppert, p. 28, pl. 13 figs 4–9.

1906 *Ulmus carpinooides* Göppert, Menzel, p. 67, pl. 4 figs 5–16a.

1988 *Ulmus carpinooides* Göppert emend. Menzel, Kovar-Eder, p. 41, pl. 7 figs 22–27.

**Material.** Coll. file nos: 1998B0014/ 439 B; 2000B0015/16 B, 22, 36, 47, 69 ?, 86 A, 106, 109, 117 B, 122, 123, 134 A, 167, 183 A, 186 A, 195, 198, 214, 215, 220, 266, 288 C, 296 H, 299, 319 D, 326 B, 327, 337, 340, 300, 355 C, 364 A, 408, 436 A ?, D, 457, 460 ?, 508.

**Description.** Lamina slightly ovate, elliptic to oblong, somewhat asymmetric, base slightly cordate, exceptionally preserved only; no apex preserved; margin distinctly, densely, double serrate; shape of teeth variable: acuminate or basal and apical sides sometimes straight, convex or concave, sinus acute, tooth apex acute; secondary veins simple craspedodromous ending in the first-order teeth, densely spaced (distances mostly between 2–4 mm), secondaries forking occasionally, first running straight across the lamina, then slightly curved towards the apex, near the margin often sending several finer veins into lower second-order marginal teeth or towards the tooth bases; higher order venation not preserved.

**Remarks.** The taxonomy of fossil elm foliage is rather complex and has been discussed by different authors, e.g. Menzel (1906), Jung (1963), Iljinskaya (1982), Kovar-Eder (1988). Here, we follow the arguments of Kovar-Eder (1988) that arrive at *Ulmus carpinooides* Göppert sensu Menzel being the correct name of this taxon. *U. carpinooides* is one of the most common azonal taxa of middle to late Miocene floras and is usually represented by many

specimens. It belongs to the few azonal taxa present in the here described assemblage. As in *Platanus leucophylla* and *Myrica lignitum*, its leaf remains are abundant (40 fragmentarily preserved specimens).

*Ulmus* pollen is documented from several levels of the Mataschen section including the upper leaf-bearing one (Meller & Hofmann 2004).

#### FAGACEAE

##### *Fagus* sp.

Pl. 2, fig. 5–6, Pl. 8, fig. 3

**Material.** Coll. file nos: 2000B0015/ 112, 118 A ?, 225 ?, 244, 331 ?, 336 ?, 381.

**Description.** Only three fragments are unambiguously assignable to this taxon, whereby only specimen no. 244 (Pl. 2, fig. 5) shows cuticle preservation. Specimen no. 112: lamina probably elliptic, 42 mm long (completed probably about 50 mm), 28 mm wide, base acute, petiole complete, 8 mm long, slightly broader at the base; midvein slender, straight, secondaries slender, originating in distances of 4–6 mm, running almost straight towards the margin, tertiaries not clearly distinguishable from the higher order venation, which forms a fine-reticulate network. Specimen no. 381 is 40 mm long and 34 mm wide, apical fragment (although its uppermost part is missing), secondaries arising in 6 to 8 mm distances, left side with one complete distinct marginal tooth and an incomplete one, basal and apical sides of teeth straight, tooth base rounded, apex acute. Specimen no. 244 (Pl. 2, fig. 6): a basal leaf fragment, base acute, midvein stout, secondaries probably pseudocraspedodromous, leaf margin only poorly preserved, gently wavy but teeth above the secondary veins not preserved.

Adaxial cuticle: not preserved.

Abaxial cuticle (Pl. 8, fig. 3): delicate, stomatal complexes anomocytic to almost cyclocytic; stomata broadly oval or sometimes nearly roundish, 19–26  $\mu\text{m}$  (23  $\mu\text{m}$ ) long, 15–21  $\mu\text{m}$  (18  $\mu\text{m}$ ) wide, stomatal aperture narrow spindle-shaped, 8–13  $\mu\text{m}$  (10  $\mu\text{m}$ ) long, poral walls of the guard cells faintly traceable; size of the non-modified epidermal cells 19–28  $\mu\text{m}$  (23  $\mu\text{m}$ ), anticlines rather variable: curved, straight, or undulate with wide sinuses, slender, less than 1  $\mu\text{m}$  thick; one-celled, well-cuti-

nized roundish trichome bases occur isolated on the slides, diameter 10–17  $\mu\text{m}$  (12  $\mu\text{m}$ ; including the thickened poral rim).

**Remarks.** Certainly, *Fagus* is present in this leaf assemblage from Mataschen. Due to the poor preservation of the foliage, however, only three specimens can be assigned unambiguously. The group of leaves described below as *Betula* vel *Fagus* sp. probably includes further leaf remains of beech. The cuticle obtained from the specimen described as ? *Fagus* vel *Sloanea* sp. (see below) resembles the cuticle of *Fagus* but is rather well preserved, thus being extremely atypical for *Fagus* (Z. Kvaček). pers. comm.

Beech pollen is documented from several levels of the profile including the upper leaf-bearing one. The fruit record also includes *Fagus*, although beech fructifications have not been detected in the upper leaf-bearing sediments (Meller & Hofmann 2004).

##### *Quercus kubinyii* (Kovats ex Etttingshausen) Czechtz

Pl. 8, fig. 4

- 1851 *Castanea kubinyi* Kováts, p. 178, nomen nudum.  
 1852 *Castanea kubinyi* Kováts, Etttingshausen, p. 6, pl. 6 fig. 12.  
 1951 *Quercus kubinyi* (Kov.) Czechtz, p. 392, fig. 7.  
 1976 *Castanea kubinyi* Kováts ex Etttingshausen; Knobloch & Kvaček, p. 35, figs 13, 14, pl. 16 figs 7–9, pl. 18 figs 1, 4–10, pl. 23 figs 4, 6, 8–11, pl. 31 fig. 7.

**Material.** Coll. file nos: 2000B0015/ 113 B; 2001B0012/469.

**Description.** Macromorphology not available.

Adaxial cuticle: thin, smooth, only small fragments preserved; non-modified epidermal cells with straight anticlines, size 19–37  $\mu\text{m}$  (27  $\mu\text{m}$ ).

Abaxial cuticle (Pl. 8, fig. 4): thin, preserved in tiny fragments only; stomatal complexes anomocytic, stomata oval, 16–20  $\mu\text{m}$  (18  $\mu\text{m}$ ) long, 12–16  $\mu\text{m}$  (14  $\mu\text{m}$ ) wide, stomatal aperture short, narrow, spindle-shaped, 4–7  $\mu\text{m}$  (5  $\mu\text{m}$ ) long, T-shaped polar thickenings developed; size of non-modified epidermal cells 12–20  $\mu\text{m}$  (15  $\mu\text{m}$ ), anticlines straight, curved or wavy; probably one-celled, roundish to oval trichome bases present but indistinct, 10–15  $\mu\text{m}$  in diameter, hypodermis composed of tiny cells, weakly discernable.

**Remarks.** Unfortunately, we report this species based only on its cuticle, but the cuticular features are significant enough for this taxonomic assignment. The cuticular features (cell size, size and shape of stomata) match very well the description given by Knobloch and Kvaček (1976). The material from Oder 2a shows a hypodermis on the adaxial cuticle but no hypodermis is described from the abaxial one. When comparing the specimen from Mataschen to the material described from Bełchatów (Worobiec 2003), the stomata are somewhat larger and a hypodermis is present on both leaf surfaces in the latter.

***“Quercus” rhenanasimilis***

Kovar-Eder **sp. n.**

Pl. 2, fig. 8, Pl. 8, figs 1–2

1975 cf. *“Quercus” lusatica* Jähnichen; Juchniewicz, pl. 4, figs 4–6.

**Holotype** selected here. Coll. file no: 2000B0015/207 – Pl. 2, fig. 8, Pl. 8, figs 1, 2.

**Type locality.** Clay pit Mataschen (“alte Grube”, 15°57'16"E/ 46°54'15"N) of the company Lias Austria GmbH, 5 km SW of Fehring, district Feldbach, Styria.

**Age.** Miocene, Lower Pannonian, mollusc “zone” B or slightly younger; mollusc “zone” B documented at the base of the sequence about 25 m below this leaf-bearing level.

**Description.** Apical part of a simple entire-margined leaf; 36 mm long (incomplete, probably twice that long), 7 mm wide (completed ? 30 mm), shape of lamina ? elliptic, apex ? acute, only the straight midvein is visible.

**Adaxial cuticle** (Pl. 8 fig. 2): rather thick, glabrous; size of non-modified epidermal cells 24–43  $\mu\text{m}$  (33  $\mu\text{m}$ ), anticlines distinct, very narrowly U to  $\Omega$ -shaped undulate, 2–4  $\mu\text{m}$  thick.

**Abaxial cuticle** (Pl. 8, fig. 1): rather thick, brittle, only small fragments preserved; type of stomatal complexes questionable because subsidiary cells not visible; stomata surrounded by an elevated ridge with lateral/radial cuticular striation, stomata large oval to roundish, 28–42  $\mu\text{m}$  (36  $\mu\text{m}$ ) long, 23–31  $\mu\text{m}$  (26  $\mu\text{m}$ ) wide, epidermal walls of guard cells sometimes hardly traceable, outer stomatal ledges of the guard cells thickened, straight, stomatal aperture a long slit almost reaching

the poles, 19–34  $\mu\text{m}$  (27  $\mu\text{m}$ ) long; anticlines of the non-modified epidermal cells not visible; big, one-celled, strongly cutinized, round trichome bases in intercostal areas present but rare, outer diameter 22–25  $\mu\text{m}$  (23  $\mu\text{m}$ ); no trichomes preserved.

**Remarks.** Due to the shape of the densely spaced stomata, which are surrounded by a strong, partly radially striated cuticular rim, this leaf fragment is certainly reminiscent of *Quercus rhenana* (Kräusel & Weyland 1950) Knobloch & Kvaček 1976. But the multicellular trichome bases of stellate hairs are absent and the adaxial cuticle shows intensive  $\Omega$ -shaped undulation. We have no doubts about the assignment to the Fagaceae family but its generic identity among evergreen members of this family is unclear.

Knobloch and Kvaček (1976) regard *Quercus lusatica* Jähnichen (Jähnichen 1966) as the younger synonym of *Illicium rhenanum* Kräusel & Weyland. They refer to the good agreement of the cuticle structures from Oder 2 a with the description given by Jähnichen (1966). In *Q. rhenana*, multicellular trichome bases are characteristic, e.g. Jähnichen (1966), Bůžek et al. (1996), Kovar-Eder (1996). The original description of Kräusel and Weyland (1950) for *Illicium rhenanum* (basonym of *Q. rhenana*) and the respective figures lack evidence for the presence of multicellular trichome bases. Moreover, the original description does not indicate the strong lateral/radial striation of the cuticular rim surrounding the stomata. The reinvestigation of the respective slide (no 6312/2) in the Senckenberg collection Frankfurt/Main (by the first author) clearly showed that these features are developed. Discrepancies in the size of stomata – according to Kräusel and Weyland (1950) 40–50  $\mu\text{m}$  “von Pol zu Pol” and to Jähnichen (1966) 47–66.3  $\mu\text{m}$ , including the ring of subsidiary cells – are due to the fact that Kräusel and Weyland (1950) also included the ring of subsidiary cells in the measurements, probably interpreting it as strongly cutinized walls of the guard cells. We have remeasured the original specimen described by Kräusel and Weyland: stomata length is 24–33  $\mu\text{m}$  (thickened rim excluded) and 36–48  $\mu\text{m}$  (thickened rim included). The stomata sizes of the specimen from the Rhineland and Luasatia, therefore match rather well.

The adaxial cuticle of *Quercus rhenana* is rather inconspicuous and bears straight/bent to undulate anticlines (Kräusel & Weyland 1950, Jähnichen 1966); it is usually poorly preserved and mostly remained unfigured. In all evidences available, they are very different from *Quercus rhenanasimilis*.

The first author viewed the material determined as *Q. rhenana* from Hrádek nad Nisou, Bohemia. Although older (middle Miocene), these leaves appear to be more similar to "*Quercus*" *rhenanasimilis* from Mataschen than to *Q. rhenana* because simple trichome bases of almost the same size and shape are scattered, while trichome bases of stellate hairs are largely absent. Moreover, the anticlines of the non-modified cells on the adaxial cuticle are undulate, although less intensively narrowly  $\Omega$ -shaped than in the leaf from Mataschen, e.g. slides PRC Kr-57, 94, 466. Unfortunately, this material remains unpublished.

Also "*Quercus*" *lusatica* Jähnichen (syn. *Q. rhenana*) from Turów (Juchniewicz 1975) shows only simple trichome bases on the lower leaf surface, largely resembling those of the Mataschen specimen. It also lacks the bases of stellate hairs, but the anticlines of the non-modified epidermal cells of the adaxial cuticle are described as curved and are clearly not strongly undulate. Possibly there is a relation to *Quercus praerhenana* Walther & Kvaček (Walther 1999).

*Q. praerhenana* has been described from Kleinsaubernitz (Saxony, late Oligocene, Walther 1999), and is differentiated from *Q. rhenana* mainly by the absence of the bases of stellate hairs. The features of the abaxial cuticle of *Q. praerhenana* match rather well those of the here-described "*Q.*" *rhenanasimilis*, but the narrowly U to  $\Omega$ -shaped undulation of the anticlines on the adaxial cuticle of the latter is most characteristic and clearly distinguishes "*Q.*" *rhenanasimilis* from *Q. praerhenana*.

Recently, Worobiec (2003) described four leaves as *Q. rhenana* from Bełchatów. The cuticles lack multicellular trichome bases of stellate hairs, a hypodermis is developed on the upper and lower surface, the stomata are less densely spaced than in *Q. rhenana*, and the radial striation of the cuticular ring surrounding the stomata which is characteristic in *Q. rhenana* has not been recognized by Worobiec. None of these features is charac-

teristic of *Q. rhenana*, indicating that we are dealing with a different species. The number of entire-margined probably evergreen Neogene Fagaceae is clearly far from being resolved.

***Trigonobalanopsis rhamnoides***  
(Rossmässler) Kvaček & Walther

Pl. 7, figs 7–8

1840 *Phyllites rhamnoides* Rossmässler, p. 35, pl. 8 figs 30, 31.

1988 *Trigonobalanopsis rhamnoides* (Rossmässler) comb. n. Kvaček & Walther, p. 405, pl. 49 figs 1–8, pls 50–54, pl. 55 figs 2–7, pl. 56 figs 1–4, pl. 57, textfigs 2–4.

Material. Coll. file nos: 1998B0014/ 438, 442, 626, 627; 2000B0015/ 42, 43, 46, 96 B, 103, 129, 362, 391, 393 D, 502 A, 612.

Description. Macromorphology extremely poorly preserved, fragments of entire-margined simple leaves elliptic; largest fragment (no. 129) 45 mm long (completed probably twice that long) and 28 mm wide, base obtuse/rounded (no. 391); midvein straight; no further macro-morphological details available.

Adaxial cuticle (Pl. 7, fig. 8): rather thin, glabrous, size of non-modified epidermal cells 12–28  $\mu\text{m}$  (16–20  $\mu\text{m}$ ), anticlines undulate, wavy, curved or straight, about 1  $\mu\text{m}$  thick.

Abaxial cuticle (Pl. 7, fig. 7): medium thick, stomatal complexes cyclocytic with 5–8 narrow, intensively staining subsidiary cells; stomata roundish to oval, hardly staining, densely spaced, more or less distinctly arranged in groups, stomata 13–23  $\mu\text{m}$  (16–19  $\mu\text{m}$ ) long, 12–21  $\mu\text{m}$  (15–17  $\mu\text{m}$ ) wide, length of the oval, roundish or rarely spindle-shaped stomatal aperture 5–10  $\mu\text{m}$  (7–9  $\mu\text{m}$ ); size of non-modified epidermal cells 7–22  $\mu\text{m}$  (12–16  $\mu\text{m}$ ), anticlines well developed, undulate, wavy or curved, up to 1  $\mu\text{m}$  thick; one-celled, well cutinized and intensively staining, round to oval trichome bases present in intercostal areas and upon veins, outer diameter 8–15  $\mu\text{m}$  (10  $\mu\text{m}$ ), their abundance is variable.

Remarks. Although more than ten specimens are available, none of them is complete. All remains have been identified only based on the unambiguous cuticle structures. *Trigonobalanopsis* pollen has also been recorded from different levels in Mataschen, including the upper leaf-bearing one. Neither cupules nor fruits have been found (Meller & Hofmann 2004).

## FAGACEAE VEL ELAEOCARPACEAE

? *Fagus* vel *Sloanea* sp.

Pl. 2, fig. 7, Pl. 8, fig. 5

Material. Coll. file no: 2000B0015/342.

**Description.** An acute leaf base, veins hardly traceable, texture firm, margin probably entire; 20 mm long (incomplete), at least 20 mm wide.

Adaxial cuticle: medium thick, glabrous, non-modified epidermal cells 21–32 µm large, anticlines not or only faintly traceable, probably undulate.

Abaxial cuticle (Pl. 8, fig. 5): medium thick, glabrous; stomatal complexes anomocytic with tendency towards cyclocytic, stomata roundish to oval, only faintly staining, 13–21 µm (18 µm) long, 12–18 µm (15 µm) wide, stomatal aperture spindle-shaped, 7–12 µm (9 µm) long; size of non-modified epidermal cells 19–35 µm (26 µm), anticlines U-shaped undulate to curved, up to 1 µm thick.

**Remarks.** The anomocytic to cyclocytic stomatal complexes remind that of Fagaceae (*Fagus*), the size and shape of the stomata as well as the undulate course of the anticlines of the non-modified epidermal cells on the adaxial and abaxial cuticle match well (see Kvaček & Walther 1991). However, the stomata are somewhat smaller than in *Fagus* sp. (19–26 µm × 15–21 µm, average 23 µm × 18 µm). Generally, beech is known to have very delicate cuticles, so we hesitate to attribute these cuticles to *Fagus*.

The genus *Sloanea* (Elaeocarpaceae), recently investigated by Kvaček et al. (2001), exhibits very similar cuticular features. In the specimen from Mataschen, the stomata are slightly larger than in the Palaeogene species *Sloanea elliptica* (Andreanszky) Kvaček & Hably, *S. artocarpites* (Ettingshausen) Kvaček & Hably, and *S. nimrodi* (Ettingshausen) Kvaček & Hably, for cuticle description see *Icaciniophyllum artocarpites* (Ettingshausen) Kvaček & Bůžek and *Icaciniophyllum nimrodi* (Ettingshausen) Kvaček & Bůžek (Kvaček & Bůžek 1995), while the variability of the stoma size in modern species of *Sloanea* (Kvaček et al. 2001) includes the dimensions represented in the here described specimen.

## BETULACEAE

cf. *Betula* sp.

Pl. 2, figs 9–10, Pl. 3, fig. 7

Material. Coll. file nos: 2000B0015/254, 306, 403.

**Description.** Tiny fragments of probably simple craspedodromous leaves, secondaries slender, originating at distances of 4–8 mm, running into marginal teeth; margin double serrate, teeth tiny, acuminate, apex and sinus acute.

**Remarks.** Unfortunately, these remains lack more diagnostic features. However, pollen of *Betula* is included in the pollen spectra of numerous samples investigated from Mataschen, including the upper leaf-bearing level (Meller & Hofmann 2004).

*Alnus menzelii* Raniecka-Bobrowska

Pl. 2, figs 11–13

1954 *Alnus menzelii* Raniecka-Bobrowska, p. 11, fig. 4, phot. 11–13.

Material. Coll. file nos: 2000B0015/120, 143 B, 304 B, C.

**Description.** Lamina slightly ovate, up to 62 mm long (incomplete), up to at least 40 mm wide, base slightly cordate, apex not preserved; margin (no. 304 C) finely serrate, basal and apical sides almost straight, tooth base and apex acute; midvein stout, secondaries arising in distances between 4 (near the base) and 9 mm, running curved (the basal ones) to almost straight (the apical ones) and diverging towards the leaf margin, tertiaries perpendicular (forked-) percurrent (no. 304 C).

Adaxial cuticle: medium thick, small fragments preserved only; size of non-modified epidermal cells 15–28 µm (22 µm), anticlines thin and straight.

Abaxial cuticle: only few, four-celled, rectangular, well-cutinized trichome bases recognizable, 19–26 µm in diameter.

**Remarks.** The four-celled trichome bases support only the generic assignment. The determination of these leaf fragments is based on their gross morphology. Especially characteristic are the general shape of the lamina and the cordate leaf-base.

*Alnus* sp.

Pl. 2, fig. 14

**Material.** Coll. file nos: 2000B0015/53 A, 81 A, B, 213, 232, 286, 341, 387 B.

**Description.** Fragments of leaves, up to 75 mm (90 mm when completed) long, 40 mm (up to 45 mm) wide, shape of lamina ovate/elliptic; petiole (no. 53 A) 22 mm long, slender, slightly curved; base obtuse (no. 53 A), with slender secondaries arising at distances of 4–8 mm, running parallel, sometimes smoothly curved towards the margin, tertiaries perpendicular (forked-) percurrent; no further details preserved.

**Remarks.** These fragments cannot clearly be assigned to the foregoing species but most probably belong to the genus *Alnus* due to the feature combination described above. Numerous pollen samples from the profile in Mataschen include *Alnus*, as does sample P21 from the upper leaf-bearing level (Meller & Hofmann 2004).

**Betulaceae** gen. et sp. indet.

Pl. 8, fig. 7

**Material.** Coll. file nos: 2000B0015/31, 51, 88 B, 108 A, 131, 307, 309 A, C, 340.

**Description.** Fragments with double serrate margin, craspedodromous venation, and secondaries not densely spaced.

Abaxial cuticle (Pl. 8, fig. 7): small fragments preserved only, anticlines of non-modified epidermal cells straight to slightly wavy, stomatal complexes anomocytic, stomatal aperture slender, spindle-shaped, occasionally pluricellular trichome bases (4–5 celled) preserved.

**Remarks:** The preservation of these remains is too poor to assign them to either of the Betulaceae genera. However, small fragments of double serrate margin, secondary venation and the pluricellular trichomes bases justify to assign them to the Betulaceae family.

## BETULACEAE VEL FAGACEAE

*Betula* vel *Fagus* sp.

**Material.** Coll. file nos: 2000B0015/11, 18, 41, 44 A, 104, 222 A, C, D, 226, 239 B, 243 A,

304 A, D, 308, 311 A, 318, 390 A, 407, 417, 432 B, 436 A, 462.

**Remarks.** Many specimens may belong to either of these genera. The poor preservation prevents a more exact assignment.

## MYRICACEAE

*Myrica lignitum* (Unger) Saporta

Pl. 2, figs 15–17, Pl. 12, figs 1–2

1847 *Quercus lignitum* sp. n., Unger, p. 113, pl. 31, figs 5–7.

1865 *Myrica lignitum* (Ung.) comb. n., Saporta, p. 102.

**Material.** Coll. file nos: 2000B0015/10 A, 96 C, 97 B ?, 125, 177, 188 D, G, 234 D, 275, 291 C, 293 A?, 302 B, 298 A, 305, 320 A, 422 B, 432 A, 452; 2001B0012/468, 476.

**Description.** Lamina long and narrow, length up to at least 100 mm when completed, width up to 10–12 mm, base distinctly decurrent, apex not preserved; leaf margin entire, slightly wavy in the apical part; on specimen no. 25 possibly one tiny acute tooth preserved; in no. 422 B the margin is possibly crenate but only fragmentarily preserved; except for the distinct midvein the venation is not visible.

Adaxial cuticle (Pl. 12, fig. 2): thin, rarely preserved; size of non-modified epidermal cells 12–23  $\mu\text{m}$  (16  $\mu\text{m}$ ), anticlines slender, straight or curved; two-celled, well-cutinized, oval to roundish trichome bases common upon veins and in intercostal areas, 12–22  $\mu\text{m}$  (15–18  $\mu\text{m}$ ) in diameter; trichomes peltate, multicellular, 59–105  $\mu\text{m}$  (76–80  $\mu\text{m}$ ) in diameter.

Abaxial cuticle (Pl. 12, fig. 1): delicate, stomatal complexes anomocytic, stomata roundish to oval, less intensively staining than the other cells, stomata 15–26  $\mu\text{m}$  (20–21  $\mu\text{m}$ ) long, 13–22  $\mu\text{m}$  (18–19  $\mu\text{m}$ ) wide, stomatal aperture broad-oval, 8–12  $\mu\text{m}$  (10  $\mu\text{m}$ ) long; non-modified epidermal cells somewhat dome-shaped, size 12–37  $\mu\text{m}$  (15–23  $\mu\text{m}$ ); anticlines straight, curved or rarely wavy; trichome bases and trichomes as on the upper leaf surface, bases 15–24  $\mu\text{m}$  (17–21  $\mu\text{m}$ ) in diameter, peltate, multicellular heads 63–104  $\mu\text{m}$  (77–89  $\mu\text{m}$ ) in diameter.

**Remarks.** Fragments of *Myrica lignitum* leaves are rather abundant in this assemblage. The cuticle features unambiguously

justify the assignment to the specific level. Fruit and pollen records of Mataschen include *Myrica* at different levels, but only pollen is also documented from the upper leaf-bearing level (Meller & Hofmann 2004).

## ACERACEAE

*Acer tricuspdatum* Bronn

Pl. 8, fig. 6

1838 *Acer tricuspdatum* Bronn, p. 865, pl. 35, figs 10a, b.

**Material.** Coll. file no: 2000B0015/48.

**Description.** One poorly preserved leaf apex: acuminate, margin probably with teeth but incompletely preserved.

Adaxial cuticle: not preserved.

Abaxial cuticle (Pl. 8, fig. 6): delicate, poorly preserved in small fragments only; stomatal complexes probably anomocytic, stomata roundish, 16–20  $\mu\text{m}$  (17  $\mu\text{m}$ ) long, 16–18  $\mu\text{m}$  (17  $\mu\text{m}$ ) wide, stomatal aperture oval, 8–12  $\mu\text{m}$  (10  $\mu\text{m}$ ) long, outer stomatal ledges of the guard cells thickened; non-modified epidermal cells dome-shaped, size 12–18  $\mu\text{m}$  (15  $\mu\text{m}$ ), anticlines curved or straight; indistinct, one-celled, round trichome bases present, 7–10  $\mu\text{m}$  in diameter.

**Remarks.** Stomata shape supports the assignment to *Acer tricuspdatum*. As the cuticle derives from the apex of a lobe, this may explain its poor preservation. *Acer* is generally rare in the pollen record. In Mataschen, maple (2 types) is documented in few samples only, including one from the leaf-bearing layer (P21, Meller & Hofmann 2004).

## NYSSACEAE

*Nyssa cf. haidingeri* (Ettingshausen)  
Kvaček & Bůžek

Pl. 12, figs 3–4

cf. 1866 *Laurus haidingeri* Ettingshausen, p. 174, pl. 30, figs 5, 8, 9.

cf. 1972 *Nyssa haidingeri* (Ettingshausen) comb. n., Kvaček & Bůžek, p. 373, figs 1, 2, pl. 1, pl. 2 figs 1, 2, pl. 3 figs 1–3, pl. 4 figs 1–5.

**Material.** Coll. file nos: 2000B0015/237, 328 B.

**Description.** A tiny fragment (no. 328 B)

and one fragment lacking base and apex (no. 237): 53 mm long, 26 mm wide, ? elliptic, base ? obtuse, apex ? acute/acuminate, ? entire-margined, midvein straight, secondaries arising at distances of 25–30 mm; no further details available.

Adaxial cuticle (Pl. 12, fig. 4): thick, well preserved, glabrous, size of non-modified epidermal cells 19–44  $\mu\text{m}$  (33  $\mu\text{m}$ ), anticlines straight or sometimes curved, 1–3  $\mu\text{m}$  thick.

Abaxial cuticle (Pl. 12, fig. 3): delicate; stomata (broad) oval, scattered, rather variable in size, 22–32  $\mu\text{m}$  (26  $\mu\text{m}$ ) long, 12–24  $\mu\text{m}$  (18  $\mu\text{m}$ ) wide, stomatal aperture broad spindle-shaped to elliptic, 17–24  $\mu\text{m}$  (20  $\mu\text{m}$ ) long, epidermal wall of the guard cells faint; anticlines of the non-modified epidermal cells not traceable; parallel, densely spaced striation developed along veins, around the stomata more or less oriented concentrically, upon non-modified epidermal cells striation wavy, running in parallel bundles, radially arranged around small, indistinct trichome bases, trichome bases about 10  $\mu\text{m}$  in diameter, no trichomes preserved.

**Remarks.** The cuticular features match quite well the specimens from Wackersdorf (Knobloch & Kvaček 1976) except for the adaxial cuticle, which is thicker in our specimens. Only tiny fragments from the area above veins are available; they are largely glabrous, and glands have not been observed. The pollen record of Mataschen includes *Nyssa* but fruits have not been found (Meller & Hofmann 2004).

## SYMPLOCACEAE

*Symplocos rara* Kovar-Eder **sp. n.**

Pl. 2, fig. 18, Pl. 10, figs 7–8

1976 *Dicotylophyllum* sp. 8, Knobloch & Kvaček, p. 83, pl. 20 fig. 4, pl. 38 figs 8–10, text-fig. 48.

**Holotype** designated here. Coll. file no. 2000B0015/115 – Pl. 2, fig. 18, Pl. 10, figs 7, 8.

**Type locality.** Clay pit Mataschen (“alte Grube”, 15°57'16"E/46°54'15"N) of the company Lias Austria GmbH, 5 km SW of Fehring, district Feldbach, Styria.

**Age.** Miocene, Lower Pannonian, mollusc “zone” B or slightly younger; mollusc “zone” B

documented at the base of the sequence about 25 m below this leaf-bearing level.

**Derivation of the name.** Indicating its rare documentation.

**Description.** The basal half of a slightly elliptic lamina, base ? acute, petiole not preserved, leaf margin entire, midvein straight, secondaries hardly visible, higher venation not discernible.

Adaxial cuticle (Pl. 10, fig. 8): medium thick, glabrous, size of non-modified epidermal cells 23–44  $\mu\text{m}$  (33  $\mu\text{m}$ ), anticlines U-shaped undulate, about 1  $\mu\text{m}$  thick.

Abaxial cuticle (Pl. 10, fig. 7): medium thick, glabrous; stomatal complexes brachyparacytic with very narrow lateral subsidiary cells, stomata roundish and densely spaced, 21–26  $\mu\text{m}$  (23  $\mu\text{m}$ ) long, 22–24  $\mu\text{m}$  (23  $\mu\text{m}$ ) wide, guard cells more intensively staining than all other cells because the outer cuticular ledges surrounding the stomatal aperture are thick but only indistinctly differentiated from the remaining cuticle above the guard cells, and the epidermal wall of the guard cells is thick as well, stomatal aperture small and roundish, 7–10  $\mu\text{m}$  (9  $\mu\text{m}$ ) long, polar T-shaped thickenings developed; size of non-modified epidermal cells 23–40  $\mu\text{m}$  (30  $\mu\text{m}$ ), anticlines U-shaped undulate, about 1  $\mu\text{m}$  thick.

**Remarks.** Although this leaf fragment lacks macro-morphological diagnostic features, the cuticle, especially the very narrow paracytically arranged subsidiary cells, point towards *Symplocos* (Kvaček 2004). The cuticle of this leaf is nearly identical with that of *Dicotylophyllum* sp. 8 from Wackersdorf sensu Knobloch & Kvaček (1976), refigured here on Plate 11, fig. 1, which Kvaček (2004) included in *Symplocos*. As in Wackersdorf, only one leaf fragment documents this species from Mataschen. Neither pollen nor fruit remains of *Symplocos* are available from Mataschen (Meller & Hofmann 2004).

#### THEACEAE

The fossils described in the following three species bear stomata of the “*Gordonia*-type” (Keng 1962). Tangentially more or less elongated and well-discernible subsidiary cells are mostly characteristic of *Gordonia* within the Theaceae. In other genera of this family, this feature is less distinct to absent.

Fruits of *Eurya stigmosa* (Ludwig) Mai have been reported from the section of Mataschen below the upper leaf-bearing level, but no Theaceae pollen record is available (Meller & Hofmann 2004).

#### *Gordonia emanuelii* Kovar-Eder, **sp. n.**

Pl. 2, figs 19–20, Pl. 9, figs 1–2, Pl. 10, fig. 1

**Holotype** selected here. Coll. file no 2000B0015/241 A – Pl. 9, figs 1, 2.

**Paratypes.** Coll. file nos: 2000B0015/28, 333, 366, 425. – Pl. 2, figs 19, 20, Pl. 10, fig. 1.

**Type locality.** Clay pit Mataschen (“alte Grube”, 15°57'16"E/46°54'15"N) of the company Lias Austria GmbH, 5 km SW of Fehring, district Feldbach, Styria.

**Age.** Miocene, Lower Pannonian, mollusc “zone” B or slightly younger; mollusc “zone” B documented at the base of the sequence about 25 m below this leaf-bearing level.

**Derivation of the name:** In honour of the late Prof. Emanuel Palamarev, palaeobotanist, who investigated, among other fossils, the remains of the Theaceae.

**Description.** Coriaceous leaves, fragmentarily preserved, base acute, lamina possibly elliptic, no apex preserved, margin ? entire, possibly wavy or with single small teeth present ?, midvein stout, no further venation details discernible.

Adaxial cuticle (Pl. 10, fig. 1): thick; size of non-modified epidermal cells 24–51  $\mu\text{m}$  (37  $\mu\text{m}$ ), anticlines straight or sometimes curved, 3–5  $\mu\text{m}$  thick; very rarely one-celled, well-cutinized, round trichome bases present in intercostal areas, outer diameter 17–22  $\mu\text{m}$  (20  $\mu\text{m}$ ), trichome base cells sometimes slightly radially elongated; trichomes not preserved;

Abaxial cuticle (Pl. 9, figs 1, 2): thick, smooth, almost glabrous, along veins faint parallel cuticular striation; stomatal complexes anisocyclocytic with 3–6 narrow, tangentially elongated, intensively staining subsidiary cells surrounding the stomata; stomata roundish to oval, quite variable in size, 22–43  $\mu\text{m}$  (27–35  $\mu\text{m}$ ) long, 22–34  $\mu\text{m}$  (25–30  $\mu\text{m}$ ) wide, outer stomatal ledges of the guard cells distinctly thickened, smooth, stomatal aperture 8–26  $\mu\text{m}$  (11–19  $\mu\text{m}$ ) long; prominent but short polar I-pieces present, often not reaching the

poles, above the guard cells 1–2 concentric striae; size of non-modified epidermal cells 21–57  $\mu\text{m}$  (28–40  $\mu\text{m}$ ), anticlines straight, curved to somewhat wavy, about 2  $\mu\text{m}$  thick.

**Remarks.** Most fossil Theaceae species described so far exhibit stronger striation or even wrinkles on the cuticles. *Gordonia pseudoknauensis* Kvaček (Kvaček 2004) from Flörsheim is somewhat similar to *G. emanuelii*. However, *G. pseudoknauensis* differs by fewer and less distinctly developed subsidiary cells (3–4), more elliptic stomata, less distinct outer stomatal ledges, the spindle-like aperture with less well-developed polar I-shaped pieces. In *Gordonia hradekensis* (Kvaček & Bůžek) Palamarev & Bozukov the stomata more closely resemble *G. emanuelii*, being almost circular to broadly elliptic, showing well-thickened outer stomatal ledges forming an oval front cavity, and having well-developed polar I-pieces. However, *G. hradekensis* differs in the lower number of subsidiary cells (3–4), the presence of trichome bases, and the striae and wrinkles covering the abaxial cuticle (Kvaček & Bůžek 1966, Kvaček & Walther 1984b, Kvaček 2004).

In ? *Gordonia oberdorfensis* Kovar-Eder described from the early Miocene of Oberdorf, N Voitsberg, Western Styria (Kovar-Eder & Meller 2001), the abaxial cuticle is covered by striae, the subsidiary cells are hardly traceable (and their number therefore unclear), the stomatal aperture is spindle-shaped with well-developed apices, and the polar I-pieces are slender.

***Gordonia pannonica* Kovar-Eder, sp. n.**

Pl. 2, figs 21–23, Pl. 9, figs 5–6, Pl. 10, fig. 3

**Holotype** selected here. Coll. file no. 2000B0015/149 – Pl. 9, fig. 5, Pl. 10, fig. 3.

**Paratypes.** Coll. file nos 2000B0015/7, 17, 143, 206, 259 – Pl. 2 figs 21–23, Pl. 9 fig. 6.

**Type locality.** Clay pit Mataschen (“alte Grube”, 15°57'16"E/ 46°54'15"N) of the company Lias Austria GmbH, 5 km SW of Fehring, district Feldbach, Styria.

**Age.** Miocene, Lower Pannonian, mollusc “zone” B or slightly younger; mollusc “zone” B documented at the base of the sequence about 25 m below this leaf-bearing level.

**Derivation of the name.** After its

occurrence in the Pannonian region of the Paratethys.

**Description.** Leaf fragments with acute/acuminate bases, 3–5 slender veins arising at the base, running steeply across the lamina, sometimes forking, no further details preserved.

**Adaxial cuticle** (Pl. 10, fig. 3): rarely preserved, thick; size of non-modified epidermal cells 27–43  $\mu\text{m}$  (32–33  $\mu\text{m}$ ), anticlines curved, slightly undulate and knobbed.

**Abaxial cuticle** (Pl. 9, figs 5, 6): well preserved, thick, glabrous; stomatal complexes cyclocytic, subsidiaries tangentially elongated, covered by concentric wrinkles; stomata 22–39  $\mu\text{m}$  (26–32  $\mu\text{m}$ ) long, 19–27  $\mu\text{m}$  (23–25  $\mu\text{m}$ ) wide, epidermal walls and outer stomatal ledges of the guard cells distinctly thickened, smooth, stomatal aperture oval, 12–22  $\mu\text{m}$  (14–18  $\mu\text{m}$ ) long, polar I-pieces more or less prominent; anticlines of the non-modified epidermal cells not visible; coarse, bundled, more or less parallel-running wrinkles strongly developed; wrinkles along veins oriented parallel to the elongated cell outlines.

**Remarks.** Although the macro-morphology of these leaves is rather poorly preserved, these blades probably exhibit an ? acrodromous venation.

Following the determination key of Kvaček and Walther (1984a) for the Theaceae, these leaves are assigned to *Gordonia* not only based on the concentrically elongated subsidiary cells but also on the almost concentrically wrinkles surrounding the stomata, and the wrinkles which are oriented in almost parallel bundles covering the areas between the stomatal complexes, and the smooth adaxial cuticle with curved and slightly undulating anticlines. The innermost circle of the concentric sculpturing of the stomatal complexes is situated above the guard cells.

While the abaxial cuticle of *Gordonia emanuelii* exhibits a rather clear and regular appearance, that of *G. pannonica* is more irregular. This general appearance is largely caused by the wrinkles developed in *G. pannonica*. Although the stomata are almost equal in length, their width is smaller in *G. pannonica* (average 23–25  $\mu\text{m}$ ) than in *G. emanuelii* (average 25–30  $\mu\text{m}$ ). Further differences pertain to the adaxial cuticles, which show

straight to slightly curved, even anticlines in *G. emanuelii* but curved to undulate, knobbed ones in *G. pannonica*.

*G. pannonica* differs from *Cleyera schilcheriana* Kovar-Eder (Kovar-Eder & Meller 2001) by the adaxial cuticle lacking striation, the presence of one distinct ring of wrinkles upon the guard cells, and the more evenly developed outer cuticular ledges forming the front cavity.

Schneider (1969, pl. 8 fig. 1) figured *Krauselicutis ingens* n. fsp., whose cuticle resembles that of *G. pannonica* regarding the concentrically elongated subsidiary cells, the circular wrinkles around and above the stomata, the polar thickenings, and the rather parallel-oriented wrinkles in the areas between the stomatal complexes. Nevertheless, there is a distinct difference in stomata size. The stomata of *Krauselicutis ingens* are distinctly bigger 37 (32–44  $\mu\text{m}$ ) than those of *G. pannonica*.

### ***Gordonia styriaca* Kovar-Eder sp. n.**

Pl. 9, figs 3–4, Pl. 10, fig. 2

1999 “*Viburnum*” *atlanticum* Ettingshausen sensu Bůžek; Walther, p. 123, pl. 13 figs 8–10.

Holotype selected here. Coll. file no 2000B0015/10 B. – Pl. 9, figs 3–4, Pl. 10, fig. 2.

Type locality. Clay pit Mataschen (“alte Grube”, 15°57'16"E/46°54'15"N) of the company Lias Austria GmbH, 5 km SW of Fehring, district Feldbach, Styria.

Age. Miocene, Lower Pannonian, mollusc “zone” B or slightly younger; mollusc “zone” B documented at the base of the sequence about 25 m below this leaf-bearing level.

Derivation of the name. From the Latin *styriacus*, indicating the occurrence in Styria, Austria.

Description. No macro-morphological details available.

Adaxial cuticle (Pl. 10, fig. 2): medium thick, glabrous, size of non-modified epidermal cells 21–43  $\mu\text{m}$  (31  $\mu\text{m}$ ), anticlines straight, sometimes curved to slightly wavy, 1–3  $\mu\text{m}$  thick.

Abaxial cuticle (Pl. 9, figs 3, 4): medium thick, smooth, stomatal complexes cyclocytic to incomplete amphicyclocytic, 5–7 subsidiary cells, partly tangentially elongated, more intensively staining, stomatal complexes partly

densely spaced, so that adjacent stomata sometimes share their subsidiary cells, stomata roundish or broadly oval, 19–27  $\mu\text{m}$  (24  $\mu\text{m}$ ) long, 17–26  $\mu\text{m}$  (21  $\mu\text{m}$ ) wide, epidermal walls and outer cuticular ledges of the guard cells thickened, stomatal aperture of variable shape and size, roundish to oval, 10–16  $\mu\text{m}$  (14  $\mu\text{m}$ ) long, no polar thickenings developed, concentric folds present upon the guard cells; size of non-modified epidermal cells 15–33  $\mu\text{m}$  (24  $\mu\text{m}$ ), anticlines straight to slightly curved or wavy, surface smooth; a single polygonal trichome base in an intercostal area preserved, 23  $\mu\text{m}$  in diameter, poral rim and radial walls of the trichome base cells more strongly cutinized; trichomes not preserved.

Remarks. The most distinctive feature of *Gordonia styriaca* is the presence of an inner and a mostly incomplete outer circle of subsidiary cells. Although not described as characteristic for the “*Gordonia*-type” of stomatal complexes in Theaceae, this feature has been observed e.g. in the modern *Gordonia axillaris* (Roxb. ex Ker) Endl. (Pl. 12 fig. 7) and *Gordonia lasianthus* L. (Pl. 12 fig. 8). However, in *G. lasianthus* the cuticle shows distinct, concentrically arranged wrinkles around and above the stomata. The cuticular structures of *G. styriaca* somewhat resemble those of *G. emanuelii*. Characteristics that differentiate *G. emanuelii* from *G. styriaca* are the fewer subsidiary cells (3 to 6) arranged in a single ring, the bigger stomata (average 27–35  $\mu\text{m} \times 25$ –30  $\mu\text{m}$ ), the longer stomatal aperture (average 11–19  $\mu\text{m}$ ), and the I-shaped polar thickenings.

*Gordonia pannonica* differs distinctly in its general appearance due to the well-developed wrinkles on the cuticular surface, as well as by its larger stomata (average 26–32  $\mu\text{m} \times 23$ –25  $\mu\text{m}$ ) and by the presence of polar I-pieces on the stomata.

From the late Oligocene of Kleinsaubernitz, Walther (1999) has described a single, macro-morphologically well preserved leaf as “*Viburnum*” *atlanticum* Ettingshausen sensu Bůžek. Contrary to the type specimen of this taxon from Lučice, formerly Lusnitz, Oligocene (Ettingshausen 1868), the cuticle structures of the leaf from Kleinsaubernitz are very well preserved. They match those of *Gordonia styriaca* in shape and size of the stomata, of the subsidiaries, and of the non-modi-

fied epidermal cells on the abaxial cuticle. The stomatal complexes are also partly densely spaced, arranged in groups, so that adjacent stomata share their subsidiary cells. Only the size of the non-modified epidermal cells on the adaxial cuticle is smaller in the specimen from Kleinsaubernitz (12–24 µm).

***Schima mataschensis* Kovar-Eder sp. n.**

Pl. 3, fig. 4, Pl. 9, figs 7, 8.

Holotype selected here. Coll. file no. 2000B0015/222 B – Pl. 3, fig. 4, Pl. 9, figs 7, 8.

Type locality. Clay pit Mataschen (“alte Grube”, 15°57'16"E/46°54'15"N) of the company Lias Austria GmbH, 5 km SW of Fehring, district Feldbach, Styria.

Age. Miocene, Lower Pannonian, mollusc “zone” B or slightly younger; mollusc “zone” B documented at the base of the sequence about 25 m below this leaf-bearing level.

Derivation of the name. After the type locality, the clay pit of Mataschen.

Description. The basal half of a simple leaf, 48 mm long (completed probably more than twice that long), 23 mm (completed at least 25 mm) wide, petiole approximately 15 mm long, basally curved; leaf base acute, leaf margin entire, midvein straight at the base, then slightly bent; one slender secondary vein preserved.

Adaxial cuticle: delicate, smooth, poorly preserved (one tiny fragment), faint striation present locally; size of non-modified epidermal cells 22–37 µm (29 µm), anticlines straight, 1–2 µm thick.

Abaxial cuticle (Pl. 9, figs 7, 8): medium thick, better preserved than the adaxial cuticle, intensively wrinkled; type of stomatal complexes unclear due to prominent, often concentric wrinkles around the stomata; stomata sunken, guard cells largely overlapped by the surrounding wrinkles, cuticle over the guard cells delicate, epidermal walls of the guard cells not visible, outer stomatal ledges delicate, stomatal aperture oval, 7–12 µm (10 µm) long; anticlines of the non-modified epidermal cells not visible; one-celled, raised, strongly cutinized, polygonal trichome bases scattered in intercostal areas, common upon veins, outer diameter 22–31 µm (25 µm), in

intercostal areas surrounded by radial striation, trichomes not preserved.

Remarks. At a first glance, this cuticle resembles *Illipophyllum thomsoni* Kräusel & Weyland (Kräusel & Weyland 1959) due to the strong and irregularly zigzag-like wrinkles. In *I. thomsoni*, however, the wrinkles are thicker and therefore more broadly spaced, and trichome bases are absent. The Theaceae affinity of this leaf is probable. Due to the strong wrinkles, the anticlines are hardly traceable, but the concentric wrinkles around the stomata suggest a cyclocytic arrangement of the subsidiaries and “*Gordonia*-type” stomata. Within the Theaceae and among those with “*Gordonia*-type” stomata, the genus *Schima* is the most likely candidate due to the strong, concentric wrinkles surrounding and even covering the stomata and the smoothly developed adaxial cuticle.

This species is distinct from all other known fossil Theaceae by the rather irregular course of the wrinkles upon the non-modified epidermal cells: they usually run more or less parallel in bundles, e.g. *Gordonia pannonica*, *G. knauensis* (Walther & Kvaček) Palamarev & Bozukov, and ? *Cleyera schilcheriana* (Kovar-Eder & Meller 2001).

ERICACEAE

***Dicotylophyllum uhudler***

Kovar-Eder sp. n.

Pl. 3, figs 1–3, 11, Pl. 11, figs 5–8

Holotype selected here. Coll. file no. 2000B0015/3 Pl. 11, figs 6, 7.

Paratypes. Coll. file nos 1998B0014/441, 551, 629, 631, 637; 2000B0015/1, 79 A, 58, 110 A, 114, 140, 150=301, 302 A, 349, 350, 430 – Pl. 3 figs 1–3, 11, Pl. 11, figs 5, 8.

Type locality. Clay pit Mataschen (“alte Grube”, 15°57'16"E/46°54'15"N) of the company Lias Austria GmbH, 5 km SW of Fehring, district Feldbach, Styria.

Age. Miocene, Lower Pannonian, mollusc “zone” B or slightly younger; mollusc “zone” B documented at the base of the sequence about 25 m below this leaf-bearing level.

Derivation of the name. From the

red wine "Uhudler" cultivated in this part of Styria.

**Description.** Often tiny fragments, lamina thin and skin-like (not splitting in tiny fragments), thin, brownish, shape asymmetric, base mostly incomplete, acute to slightly obtuse, apex acute/acuminate, leaf margin entire, oblong (no. 441), slightly ovate (no. 114, Pl. 3, fig. 2), obovate (no. 110); largest fragment 85 mm (completed about 92 mm) long; venation brochidodromous, in no. 110 ? basally acrodromous, veins generally slender, secondaries irregularly spaced (from basal towards apical adjacent ones 13/5/8 mm), course slightly irregular, forming loops with adjacent secondaries in the marginal third of the lamina, tertiaries forming distinct, irregular meshes; fourth-order veins forming a quadro-, penta-, hexagonal network, fifth-order veins forming polygonal areoles without free-ending veinlets.

Adaxial cuticle (Pl. 11, fig. 8): thick, less frequently and less well preserved than the abaxial cuticle, smooth; size of non-modified epidermal cells 15–29  $\mu\text{m}$  (22–24  $\mu\text{m}$ ), anticlines straight, curved to undulate, unequally 2–3  $\mu\text{m}$  thick, with nodules; ? trichome or ? gland bases rare in intercostal areas and upon veins, two-celled, very strongly cutinized, oval to roundish, outer diameter 21–29  $\mu\text{m}$  (24–27  $\mu\text{m}$ )  $\times$  16–20  $\mu\text{m}$  (19  $\mu\text{m}$ ); trichomes not preserved

Abaxial cuticle (Pl. 3, fig. 11, Pl. 11, figs 5, 6): thick, well preserved, strongly wrinkled; stomatal complexes slightly elevated, neither non-modified nor subsidiary cells distinguishable; stomata 19–31  $\mu\text{m}$  (23–25  $\mu\text{m}$ ) long, 17–26  $\mu\text{m}$  (19–22  $\mu\text{m}$ ) wide, outer stomatal ledges of the guard cells distinctly thickened, smooth, stomatal aperture (broad) oval, 8–17  $\mu\text{m}$  (11–14  $\mu\text{m}$ ) long, polar slender I-pieces developed; anticlines of the non-modified epidermal cells usually not visible due to dense, randomly oriented wrinkles, only occasionally, ? undulate anticlines faintly discernible, more slender than on the adaxial cuticle; oval to roundish bases of probably ? glands / glanduliferous trichomes, mostly two-celled, sometimes three-celled, cells unequal in size; occasionally at least two stories of base cells observable; exceptionally preserved a club-shaped two-celled terminal head; these bases more abundant than on the adaxial cuticle, outer diameter of the bases 21–28  $\mu\text{m}$  (24–25  $\mu\text{m}$ )

$\times$  17–24  $\mu\text{m}$  (19–21  $\mu\text{m}$ ), wrinkles around them radially oriented.

**Remarks.** The stomatal complexes could refer to *Ilex* and Ericaceae, but *Ilex* has to be excluded because its leaves are mostly glabrous. According to Metcalfe and Chalk (1979), the stomatal complexes are anomocytic in the Ericaceae. For the Vaccinioideae, paracytic stomatal complexes are characteristic, but the cyclocytic type also occurs among the Ericaceae (Kvaček & Walther 1990). Due to the thick and dense wrinkles, the type of stomatal complexes remains ambiguous in the here-described specimens, but the anomocytic or cyclocytic arrangement seems probable. The trichome / gland bases and trichomes in the Ericaceae are manifold (Metcalfe & Chalk 1979): two-celled trichome bases of biserrate hairs occur as well as bases with two and even more stories of base cells embedded in the cuticle. The trichome bodies also include club-shaped ones as observed in the holotype. As the trichomes themselves are only very rarely preserved, we lack information about their variability. A classification key of the Ericaceae including trichome characteristics has been provided by Braun (1933). Accordingly, both multicellular club-shaped trichomes and anomocytic stomata are developed in *Arbutus unedo* L., *Arcostaphylos alpina* Niedenzu, *Kalmia latifolia* L., and *K. angustifolia* L. Those in *Kalmia* more closely resemble the fossils but the club-shaped heads consist of several cells.

The stomata of *Kalmiophyllum marcodurensense* Kräusel & Weyland (Kräusel & Weyland 1959) and *Kalmia marcodurensis* (Kräusel & Weyland) Litke (Litke 1966) resemble the here-investigated fossils, but are smaller (19–21  $\mu\text{m}$ ). Glandular trichomes consist of several short cells, thus not resembling the glandular trichome figured here (Pl. 11, fig. 7). Multi-celled trichome bases have not been described for *Kalmia marcodurensis*. Instead of thick wrinkles, only striation is developed on the cuticle of the lower leaf surface, so that the anticlines of the non-modified epidermal cells are well traceable. In *Kalmiophyllum marcodurensense* Kräusel & Weyland described by Mai and Walther (1991) the stomata are larger (21–30  $\mu\text{m} \times$  22–28  $\mu\text{m}$ , average 25.3  $\times$  24.5  $\mu\text{m}$ ), thus matching better the here described leaves, but the other features differ from those described above.

The stomata of *Kalmia saxonica* Litke

(Litke 1968) as well as of *Kalmia cf. saxonica* Litke (Worobiec 2003) differ above all by the distinctly shorter, rather round stomatal aperture and the absence of wrinkles on the abaxial cuticle. Glandular trichomes consisting of several short cells have been described by Litke, but their structure does not match the trichome described here. Worobiec described two-celled trichome bases surrounded by the radially elongated and strongly cutinised cells. The material was reviewed by the first author in the course of the present investigation, and the trichome bases include also three- to four-celled ones, thus referring to the complexity of the trichomes characteristic of the Ericaceae. They are less common than on the described leaf material from Mataschen.

Pollen of Ericaceae are documented from several samples of the Mataschen outcrop (Meller & Hofmann 2004).

#### OLEACEAE

##### *Oleinites cf. liguricus* Sachse

Pl. 3, fig. 6, Pl. 11, figs 2–4

Material. Coll. file nos: 2000B0015/ 13 B, 426, 435, 609.

**Description.** Leaf fragments almost lacking macro-morphological characteristics; only specimen no. 426 (Pl. 3, fig. 6) clearly shows a thin, skin-like shiny brownish texture, the probably entire leaf margin and the brochidodromous secondaries (5 mm apart), running in wide curves smoothly towards the leaf margin, forming loops near it; tertiaries form a polygonal network, as do the higher order veins, no free veinlets visible in the areoles; largest fragment 40 mm long (incomplete), 30 mm wide (incomplete).

Adaxial cuticle (Pl. 11, fig. 3): delicate, faintly striate; size of non-modified epidermal cells 18–28  $\mu\text{m}$  (24  $\mu\text{m}$ ), anticlines (U-shaped) undulate, about 1  $\mu\text{m}$  thick; one-celled, strongly cutinized, roundish trichome bases scattered in intercostal areas, outer diameter 8–13  $\mu\text{m}$  (10  $\mu\text{m}$ ); trichomes peltate, multicellular, 39–57  $\mu\text{m}$  (46  $\mu\text{m}$ ) in diameter.

Abaxial cuticle (Pl. 11, figs 2, 4): delicate, well preserved; stomatal complexes probably anomocytic, but surrounded by a very narrow, slightly more intensively staining ring, stomata almost round, guard cells only

faintly staining, stomata rather densely spaced, 15–21  $\mu\text{m}$  (16–18  $\mu\text{m}$ ) long, 15–20  $\mu\text{m}$  (16–18  $\mu\text{m}$ ) wide, outer stomatal ledges of the guard cells moderately thickened, stomatal aperture small roundish to broad oval, 5–9  $\mu\text{m}$  (6–7  $\mu\text{m}$ ) long; very short and slender I-pieces at the poles developed; size of non-modified epidermal cells 15–31  $\mu\text{m}$  (23  $\mu\text{m}$ ), anticlines narrow U-shaped undulate, sometimes hardly traceable; one-celled trichome bases as on the adaxial cuticle, rare in intercostal areas, outer diameter 10–15  $\mu\text{m}$  (11–13  $\mu\text{m}$ ); multicellular peltate trichomes 41–68  $\mu\text{m}$  (50  $\mu\text{m}$ ) in diameter.

**Remarks.** At a first glance the cuticular features, especially the stomata, resemble *Myrica*. However, the stomatal aperture is shorter, and the trichome bases are only one-celled and distinctly smaller than in *Myrica*. The peltate trichomes are smaller as well. The faint cuticular striation may serve as a further feature that is not characteristic of *Myrica*.

Sachse (2001) recently described *Oleinites liguricus* from Messinian deposits in the Ligurian-Piemontese Basin in northern Italy. While our material is macro-morphologically much more poorly preserved than the leaves investigated by Sachse, the cuticles of the Mataschen fragments are in a much better state than in the Italian material (which has been viewed in the course of this investigation by the first author). Our material therefore distinctly shows the relevant cuticular features. The “weakly cutinised guard cells bordered by elevated cell margins with a generally strongly cutinised tooth-like ornamentation and T-pieces” (Sachse, 2001) are discernible only when examining the inner surface of the abaxial cuticle via SEM (Sachse 2001); they are not visible in transparency light microscopy, where the stomata appear surrounded by a very narrow, slightly more intensively staining ring. Although Sachse does not indicate the size of the non-modified epidermal cells of the specimens from Torre Sterpi, the Mataschen material exhibits definitely larger-sized non-modified epidermal cells with distinctly undulate anticlines on the abaxial cuticle and similar, even larger-sized ones on the adaxial cuticle. We therefore refrain from assigning the Mataschen specimens unambiguously to *Oleinites liguricus*. *Oleinites hallbaueri* (Mai) Sachse from the early Oligocene of Seifhensdorf (Mai 1963, Sachse 2001) shows few

similarities to the here investigated material. *O. maii* (Bůžek, Holý & Kvaček) Sachse (Bůžek et al. 1976, Sachse 2001) from the early Oligocene of Markvartice resembles more closely in stoma shape and size but its cuticles are very delicate, stomata and non-modified epidermal cells are only vaguely visible and adaxially as well as abaxially, the anticlines of the non-modified cells are straight/bent but not undulate. Although Sachse thoroughly investigated modern members of the Oleaceae, he was unable to assign the fossil taxon unambiguously to a modern genus.

Regarding the pollen and fruit spectra of Mataschen, the Oleaceae record is restricted to *Fraxinus* in the pollen spectrum (Meller & Hoffmann 2004).

#### DICOTYLEDONEAE, FAM. ET GEN. INDET.

##### cf. *Dicotylophyllum dieteri* Kovar-Eder

Pl. 12, figs 5–6

cf. 1996 *Dicotylophyllum* sp. 12; Knobloch & Kvaček, p. 66, pl. 20 figs 4–7.

cf. 2001 *Dicotylophyllum dieteri* Kovar-Eder; Kovar-Eder & Meller, p. 90, pl. 1 figs 18–26, pl. 4 figs 8–15.

**Material.** Coll. file nos: 2000B0015/504 A.

**Description.** A small, legume-like leaf, lamina elliptic, base and apex incomplete, base probably rounded or obtuse, 16 (completed about 18) mm long, 10 mm wide, entire-margined except for single very tiny teeth in the upper part, no further details available.

Adaxial cuticle (Pl. 12, fig. 6a): rather thick but brittle, splitting in small fragments; size of non-modified epidermal cells 32–62  $\mu\text{m}$  (50  $\mu\text{m}$ ), anticlines widely U-shaped undulate, 2–3  $\mu\text{m}$  thick.

Abaxial cuticle (Pl. 12, fig. 5, 6b): medium thick; stomatal complexes possibly anomocytic, no subsidiary cells discernible, stomata oval, 26–37  $\mu\text{m}$  (29  $\mu\text{m}$ ) long, 19–29  $\mu\text{m}$  (22  $\mu\text{m}$ ) wide, epidermal walls of the guard cells faint, outer stomatal ledges of the guard cells slightly thickened, forming the spindle-shaped to oval stomatal aperture, which is 15–21  $\mu\text{m}$  (18.5  $\mu\text{m}$ ) long, guard cells occasionally still preserved; anticlines of the non-modified epidermal cells hardly visible, ? undulate; one-celled, round trichome bases with a very strongly cutinized, smooth poral rim, scattered, outer diameter 21–28  $\mu\text{m}$  (24  $\mu\text{m}$ ); only

two peltate unicellular shields with 55  $\mu\text{m}$  and 98  $\mu\text{m}$  in diameter preserved.

**Remarks.** This leaf closely matches those of *Dicotylophyllum dieteri* known so far from Oberdorf (Kovar-Eder & Meller 2001) and Mydlovary (Knobloch & Kvaček 1996, there as *Dicotylophyllum* sp. 12). The leaf from Mataschen differs only in having larger stomata (26–37 (mean 29)  $\mu\text{m}$   $\times$  19–29 (mean 22)  $\mu\text{m}$ ), whereas the stomata of the leaves from Oberdorf measure 18–24  $\mu\text{m}$   $\times$  12–19  $\mu\text{m}$  and in the leaf from Mydlovary are 15–25  $\mu\text{m}$  long. Based on leaf shape and venation, Knobloch & Kvaček (1976) recognized relations to the Leguminosae. The leaf fragment from Mataschen lacks further diagnostically relevant details.

#### SMILACACEAE

##### *Smilax* cf. *protolanceaefolia* Kolakovsky

Pl. 3, fig. 5, Pl. 10, figs 4–6

? 1976 *Smilax protolanceaefolia* Kolakovsky; Kolakovsky & Shakryl, p. 105, pl. 1 fig. 8.

2003 *Smilax* cf. *protolanceaefolia* Kolakovsky; Worobiec, p. 52, fig. 7: 4, pl. 23 figs 3, 3a.

**Material.** Coll. file no: 2000B0015/347.

**Description.** Basal half of a simple leaf, 33 mm long (completed probably twice that long), 30 mm wide; base rounded (? obtuse), shape of lamina probably elliptic, margin entire, except for the midvein one further preserved vein arising at the base, running steeply across the lamina, no further details visible.

Adaxial cuticle (Pl. 10, fig. 4): thick, glabrous, size of non-modified epidermal cells 38–76  $\mu\text{m}$  (56  $\mu\text{m}$ ), anticlines broadly and deeply U-shaped or sometimes moderately  $\Omega$ -shaped undulate, 1  $\mu\text{m}$  thick.

Abaxial cuticle (Pl. 10, figs 5, 6): thick, glabrous, type of stomatal complexes ? paracytic, stomata (or stomatal complexes) wide oval to rhomboidal, hardly staining, widely spaced, 19–24  $\mu\text{m}$  (21  $\mu\text{m}$ ) long, 15–18  $\mu\text{m}$  (16  $\mu\text{m}$ ) wide, epidermal walls of the guard cells hardly recognizable; outer stomatal ledges of the guard cells strongly thickened, smooth, enclosing the narrow, spindle-shaped stomatal aperture, which is 16–21  $\mu\text{m}$  (18  $\mu\text{m}$ ) long; size of the non-modified epidermal cells 32–50  $\mu\text{m}$  (42  $\mu\text{m}$ ), anticlines mostly U to  $\Omega$ -shaped undulate, undulation usually not as wide and deep as on the adaxial cuticle, 1  $\mu\text{m}$  thick, parallel

cuticular striation developed along veins and occasionally in intercostal areas.

**Remarks.** At a first glance, the cuticle may be mistaken for *Laurus abchasica*. However, in the here described specimen, the stomatal aperture is longer and distinctly spindle-shaped, neither the epidermal wall of the guard cells nor that of the subsidiaries are discernible, cuticular striation is developed, and the non-modified cells of the adaxial cuticle are larger than in *L. abchasica*.

*Smilax protolanceaefolia* has been described based on macro-morphology from Abchasia (middle/late Miocene) by Kolakovsky & Shakryl (1976). Later, Worobiec (2003) assigned a leaf from Bełchatów (level KRAM-P 217, Upper Miocene) to this taxon and described the cuticle. The specimen from Mataschen is poor in macro-morphological characteristics; the number and origin of the veins at the leaf base are incompletely preserved. Therefore, the venation type is hard to determine: it may be campylodromous but the (basal)acrodromous type cannot be excluded. The cuticle of this leaf fragment closely matches that of the leaf from Bełchatów. Worobiec mentions a macro-morphological comparison with *Majanthemophyllum*. The cuticle of *M. petiolatum* Weber differs significantly in the type of the stomatal complexes, which are cyclocytic to pericytic. Moreover, the outer walls of the guard cells are thick and distinctly developed, while the stomatal aperture is rather indistinct in *M. petiolatum* (e.g. *M. petiolatum*, Kleinsaubernitz, Saxony, Walther 1999: p. 137, pl. 18 fig. 6).

MONOCOTYLEDONEAE, FAM. ET GEN. INDET

*Monocotyledoneae* gen. et sp. indet.

**Material.** Coll. file no: 2000B0015/ 459.

**Description.** A tiny leaf fragment with parallel venation, 11 mm wide.

#### TAPHONOMIC CONSIDERATIONS

The plant remains investigated here derive from an interval of approximately 1 m sediment thickness (see page 161 and Fig. 3) The list of determined taxa are presented on Table 1. Sample coll. file no. 2000B0015 (the lower part of this interval) is most rich in specimens (371) and determined taxa (37).

Sample coll. file no. 1998B0014, collected from a thin layer above the foregoing one, yielded well-preserved specimens of 7 taxa: *Daphnogene polymorpha*, *Laurophyllum pseudoprinceps*, *Buxus pliocenica*, *Trigonobalanopsis rhamnoides*, *Viscum morlotii*, *Ulmus carpinoides*, and *Dicotylophyllum uhudler*. In sample coll. file no. 2001B0012, only 3 taxa (4 leaves) have been determined: *Daphnogene polymorpha*, *Quercus kubinyii*, and *Myrica lignitum*. As sample coll. file no. 2000B0015 is the specimen-richest and the samples coll. file nos 1998B0014 and 2001B0012 yielded fewer leaf remains, and all taxa determined from them are also present in sample 2000B0015, it is not possible to delineate any changes in the floristic spectra between the different levels. However, the layer from which coll. file no. 1998B0014 was sampled seems to be an agglomeration of taxa with leathery blades, which are more resistant against destruction than taxa with chartaceous leaves.

The sliding nature of the hanging wall observed in the field is taphonomically relevant. The leaf material may have been fragmented by transport before being embedded in the sediment and/or by the sliding nature of the plant-bearing sediments near the outcrop. Woody plants with chartaceous (deciduous) foliage are less diverse and less well-preserved than those with coriaceous (mostly evergreen) foliage. This is remarkable because, as proved by the fossil record, late Miocene azonal vegetation was dominated by deciduous woody plants: although mostly soft-leaved, they usually had a high fossilisation potential because they grew close to depositional environments. The large number of most probably evergreen taxa, and the poorer preservation of probably deciduous ones, indicate a stronger allochthonous impact on this assemblage than for other floras in the region, e.g. assemblages of Mataschen – base of the Feldbach Formation (Kovar-Eder 2004), Wörth (Kovar-Eder & Krainer 1990), Reith near Unterstorcha (Kovar-Eder & Krainer 1991), Paldau (Krenn 1998, Gross 1998), Höllgraben near Weiz (Kovar-Eder & Krainer 1988).

#### SOCIOLOGICAL IMPLICATIONS

The here investigated taphocoenosis includes only few azonal taxa: *Glyptostrobus europaeus*, *Acer tricuspdatum*, *Alnus menzelii*, *Alnus* sp.,

**Table 1.** The leaf flora of Mataschen, abundance of taxa in the different samples. Numbers in brackets indicate ambiguous determinations

Taxa identified	Coll. file no. 2000B0015/	Coll. file no. 1998B0014/	Coll. file no. 2001B0012/	Number of specimens	
Cupressaceae	<i>Glyptostrobus europaeus</i>	6		6	
Aceraceae	<i>Acer tricuspidatum</i>	1		1	
Betulaceae	<i>Alnus menzelii</i>	4		4	
Betulaceae	<i>Alnus</i> sp.	8		8	
Betulaceae	cf. <i>Betula</i> sp.	3		3	
Betulaceae	Betulaceae gen.et sp. indet.	9		9	
Betulaceae vel Fagaceae	<i>Betula</i> vel <i>Fagus</i> sp.	22		22	
Buxaceae	<i>Buxus pliocenica</i>	45	13	58	
Ericaceae	<i>Dicotylophyllum uhudler</i>	11	5	16	
Fagaceae	<i>Fagus</i> sp.	3 (+4)		3 (+4)	
Fagaceae	<i>Quercus kubinyii</i>	1	1	2	
Fagaceae	„ <i>Quercus</i> ” <i>rhenanasimilis</i>	1		1	
Fagaceae	<i>Trigonobalanopsis rhamnoides</i>	11	4	15	
Fagaceae vel Elaeocarpaceae	? <i>Fagus</i> vel <i>Sloanea</i> sp.	1		1	
Hamamelidaceae	? <i>Corylopsis</i> sp.	1		1	
Hamamelidaceae	cf. <i>Distylium heinickei</i>	3		3	
Lauraceae	<i>Daphnogene polymorpha</i>	67	3	71	
Lauraceae	<i>Laurus abchasica</i>	6		6	
Lauraceae	<i>Laurophyllum pseudoprinceps</i>	30	2	32	
Lauraceae	<i>Laurophyllum pseudovillense</i>	1		1	
Lauraceae	<i>Laurophyllum</i> sp.	1		1	
Magnoliaceae	<i>Magnolia liblarensis</i>	6		6	
Myricaceae	<i>Myrica lignitum</i>	16 (+2)	2	18 (+2)	
Nyssaceae	<i>Nyssa</i> cf. <i>haidingeri</i>	2		2	
Oleaceae	<i>Oleinites</i> cf. <i>liguricus</i>	4		4	
Platanaceae	<i>Platanus leucophylla</i>	32 (+9)		32 (+9)	
Rosaceae	<i>Rosa</i> sp.	3		3	
Symplocaceae	<i>Symplocos rara</i>	1		1	
Theaceae	<i>Gordonia emanuelii</i>	5		5	
Theaceae	<i>Gordonia pannonica</i>	7		7	
Theaceae	<i>Gordonia styriaca</i>	1		1	
Theaceae	<i>Schima mataschensis</i>	1		1	
Ulmaceae	<i>Ulmus carpinoides</i>	36 (+3)	1	37 (+3)	
Viscaceae	<i>Viscum morlotii</i>	2	1	3	
Dicotyledoneae indet.	cf. <i>Dicotylophyllum dieteri</i>	1		1	
Monocotyledoneae	Monocotyledoneae indet.	1			
Smilacaceae	<i>Smilax</i> cf. <i>protolanceaefolia</i>	1		1	
	38 taxa determ. in number of specimens	372	29	4	404
	sampled specimens	> 500	42	9	> 550
	undetermined specimens	> 130	13	5	> 150

cf. *Betula* sp., *Myrica lignitum*, *Platanus leucophylla*, *Ulmus carpinoides*, and possibly also partly *Daphnogene polymorpha* and *Nyssa* cf. *haidingeri*. With few exceptions (*Daphnogene polymorpha*, *Platanus leucophylla*, *Ulmus carpinoides*), their remains are not abundant and mostly restricted to a single or few speci-

mens (*Glyptostrobus europaeus*, *Acer tricuspidatum*, *Alnus*, *Nyssa* cf. *haidingeri*). Neither *Fraxinus*, *Populus* nor *Salix*, which are the most characteristic azonal taxa in (late) Miocene floras, have been detected in this assemblage, and *Acer* is documented by a single, tiny fragment only (*Acer tricuspidatum*).

Contrasting the record of azonal taxa, the diversity of zonal ones is very high: *Buxus pliocenica*, partly *Daphnogene polymorpha*, cf. *Distylium heinickei*, *Fagus*, *Laurophyllum pseudoprinceps*, *L. pseudovillense*, *Laurus abchasica*, *Magnolia liblarensis*, *Quercus kubinyii*, *Symplocos rara*, *Trigonobalanopsis rhamnoides*, and cf. *Dicotylophyllum dieteri*. Moreover, some of these species are rather abundant: *Buxus pliocenica*, *Daphnogene polymorpha*, *Laurophyllum pseudoprinceps*, *Trigonobalanopsis rhamnoides*. Except for *Fagus*, possibly *Magnolia liblarensis*, and *Quercus kubinyii*, most of them were evergreen. The taxa described here for the first time (*Dicotylophyllum uhudler*, *Gordonia emanuelii*, *G. pannonica*, *G. styriaca*, *Schima mataschensis*, “*Quercus*” *rhenanasimilis*) may be interpreted as (most probably evergreen) hinterland species rather than woody plants of azonal habitats because none of them has been recorded before from the rich middle/late Miocene floral record of fluviatile/lacustric/brackish environments in the Paratethys region.

In other terms, this plant assemblage from Mataschen yields, among others, 5 species of Lauraceae, at least one evergreen Fagaceae (*Trigonobalanopsis rhamnoides*), and probably a second evergreen one (“*Quercus*” *rhenanasimilis*), four species of Theaceae, *Symplocos rara*, a probably evergreen Ericaceae (*Dicotylophyllum uhudler*), and *Smilax* (*S. cf. protolanceaefolia*). In this respect, this assemblage more closely resembles floras of the early to early middle Miocene of Central Europe – often characterized as “Younger Mastixioid floras” sensu Mai – rather than floras of the late middle to late Miocene of the Central Paratethys region (see chapter “The flora of Mataschen in the European floristic context”).

#### THE LEAF, DIASPORE, AND POLLEN RECORD OF MATASCHEN IN COMPARISON

The sediments of the Feldbach Formation in Mataschen yield a leaf assemblage at the base (Kovar-Eder 2004) and one at the top, the latter being described here; at different levels, the sediments also yield fruits and pollen (Meller & Hofmann 2004; see also Figure 3, and Table 2). In the diaspore spectrum

of the whole section, the proportion of wetland taxa (hydrophytes, helophytes, woody plants) is rather high. Although poorly preserved, the pollen flora is distinctly richer than the diaspore flora.

The plant-bearing sediments at the base of the Feldbach Formation have been investigated earlier (Kovar-Eder 2004, Meller & Hofmann 2004). There, the leaf spectrum is of largely autochthonous origin, characterized by low species diversity, but single taxa are extremely specimen-rich. The plant remains are densely packed together and are macro-morphologically better preserved than the leaf material from the here-described assemblage. However, the cuticle preservation is poorer in the assemblage from the base, a condition probably related to bioturbation (Kovar-Eder 2004). The identified taxa are all azonal ones indicating swampy environment: “*Pteris*” *oeningensis* Unger, *Glyptostrobus*, *Juglans acuminata* Al. Braun ex Unger, *Myrica*, *Salix*, and monocotyledonous leaves. The diaspore spectrum of the basal sediments (sample D11) yields additional woody wetland taxa, e.g. *Cephalanthus*, *Rubus*, *Sambucus*, but also a few remains of taxa that more likely represent zonal ones (*Swida*, *Toddalia maii* Gregor, *Zanthoxylum*, single specimens of the latter two), and numerous aquatic plants such as *Trapa silesiaca* Göppert. Pollen sample P23b from the basal plant-bearing layers is among the most diverse samples from Mataschen and includes numerous azonal and zonal woody taxa: Cupressaceae (former Taxodiaceae), *Abies*, *Pinus*, *Cathaya*, *Picea*, *Tsuga*, *Acer*, *Alnus*, *Betula*, *Buxus*, *Carpinus*, *Carya*, *Castanea/Lithocarpus*, *Celtis*, Empetraceae, *Engelhardia*, Ericaceae, *Fagus*, *Fraxinus*, Hamamelidaceae, *Ilex*, *Liquidambar*, *Lonicera*, *Myrica*, *Nyssa*, *Pterocarya*, *Quercus*, *Reevesia*, *Salix*, Styracaceae, *Trigonobalanopsis*, *Ulmus*, *Vitis*, and *Zelkova*.

The woody taxa documented in samples D1, D3-D9 from the interval between the basal and the upper leaf-bearing levels of the exposure (Fig. 3) represent azonal habitats (*Alnus*, *Sambucus*, *Myrica*) or may be assigned to either wetland or hinterland environments (*Liquidambar*, *Carpinus*, *Corylus*, *Carya*, and *Liriodendron*), or probably constitute true hinterland taxa (*Broussonetia*, *Eurya stigmosa*, *Fagus deucalionis*, Lauraceae, *Paulownia cantalensis*). Some of them are documented by

**Table 2.** Comparison of the floristic spectra based on the leaf, fruit, and pollen record; leaves: Kovar-Eder (2004) and this paper; fruits, diaspores: Meller & Hofmann (2004). Taxa recorded exclusively from layers other than the upper leaf-bearing one given in brackets

Family	Pollen record	Fruit record	Leaf record
Osmundaceae	<i>Osmunda</i>		
Polypodiaceae	Polypodiaceae		
Pteridaceae	Pteridaceae		(„ <i>Pteris</i> ” <i>oeningensis</i> )
Fam. indet. (Pteridophyta)	(Pteridophyta)		
Lycopodiaceae	( <i>Lycopodium</i> / <i>Lycopodiella</i> )		
Selaginellaceae	<i>Selaginella</i>	( <i>Selaginella</i> )	
Cupressaceae		<i>Glyptostrobus europaeus</i>	<i>Glyptostrobus europaeus</i>
	<i>Sciadopitys</i>		
	Cupressaceae		
Pinaceae	<i>Abies</i>		
	<i>Cathaya</i>		
	( <i>Cedrus</i> )		
	<i>Picea</i>		
	<i>Pinus</i>		
	<i>Tsuga</i>		
Aceraceae	<i>Acer</i>		<i>Acer tricuspidatum</i>
Actinidiaceae		( <i>Actinidia</i> sp.)	
Altingiaceae	<i>Liquidambar</i>	( <i>Liquidambar</i> sp.)	
Aquifoliaceae	(Aquifoliaceae)		
Araliaceae	(Araliaceae)	(Araliaceae)	
Asteraceae	Asteraceae		
	( <i>Artemisia</i> )		
Betulaceae	<i>Alnus</i>	( <i>Alnus</i> sp.)	<i>Alnus menzelii</i>
			<i>Alnus</i> sp.
	<i>Betula</i>		cf. <i>Betula</i> sp.
			Betulaceae gen.et sp. indet.
	<i>Carpinus</i>	<i>Carpinus</i> sp.	
		( <i>Corylus</i> sp.)	
Buxaceae	<i>Buxus</i>		<i>Buxus pliocenica</i>
Caprifoliaceae	( <i>Lonicera</i> )	( <i>Sambucus</i> sp.)	
Caryophyllaceae	Caryophyllaceae		
Ceratophyllaceae		( <i>Ceratophyllum</i> sp.)	
Cercidiphyllaceae	( <i>Cercidiphyllum</i> )		
Chenopodiaceae	(Chenopodiaceae)		
Convolvulaceae	<i>Calystegia</i>		
Cornaceae	<i>Cornus</i>	( <i>Swida</i> sp.)	
Empetraceae	Empetraceae		
Ericaceae	Ericaceae	(cf. Ericaceae)	<i>Dicotylophyllum uhudler</i>
Euphorbiaceae		(Euphorbiaceae)	
Fagaceae	<i>Fagus</i>	( <i>Fagus deucalionis</i> )	<i>Fagus</i> sp.
	<i>Castanea</i> / <i>Lithocarpus</i>		
	<i>Quercus</i>		<i>Quercus kubinyii</i>
			„ <i>Quercus</i> ” <i>rhenanasimilis</i>
	<i>Trigonobalanopsis</i>		<i>Trigonobalanopsis rhamnoides</i>
Fagaceae vel Elaeocarpaceae			? <i>Fagus</i> vel <i>Sloanea</i> sp.
Haloragaceae	( <i>Myriophyllum</i> )	( <i>Proserpinaca</i> sp.)	
Hamamelidaceae	(Hamamelidaceae)		cf. <i>Distylium heinickei</i>
			? <i>Corylopsis</i> sp.
Hypericaceae ?		( <i>Hypericum</i> cf. <i>holyi</i> vel <i>Carpolithes dorofeevii</i> )	

Table 2. Continued

Family	Pollen record	Fruit record	Leaf record
Juglandaceae	<i>Carya</i>	( <i>Carya</i> sp.)	
	<i>Juglans</i>		( <i>Juglans acuminata</i> )
	<i>Pterocarya</i>		
	<i>Engelhardia</i>		
Lamiaceae		(cf. <i>Ajuga</i> sp.)	
Lauraceae			<i>Daphnogene polymorpha</i>
			<i>Laurophyllum pseudoprinceps</i>
			<i>Laurophyllum pseudovillense</i>
			<i>Laurophyllum</i> sp.
		(cf. Lauraceae)	<i>Laurus abchasica</i>
Lythraceae	<i>Decodon</i>	( <i>Decodon globosus</i> )	
		( <i>Microdiptera</i> sp.)	
Magnoliaceae		( <i>Liriodendron geminata</i> )	
		( <i>Magnolia</i> sp.)	<i>Magnolia liblarensis</i>
Mastixiaceae	( <i>Mastixia</i> )		
Menispermaceae		( <i>Sinomenium cantalense</i> )	
Moraceae		( <i>Broussonetia</i> sp.)	
		( <i>Ficus potentilloides</i> )	
Myricaceae	<i>Myrica</i>	( <i>Myrica</i> sp.)	( <i>Myrica</i> sp.)
			<i>Myrica lignitum</i>
Myrtaceae	(Myrtaceae)		
Nymphaeaceae		(cf. <i>Eoeryale</i> sp.)	
		( <i>Nymphaea</i> sp.)	
Nyssaceae	<i>Nyssa</i>		<i>Nyssa</i> cf. <i>haidingeri</i>
Oleaceae	<i>Fraxinus</i>		<i>Oleinites</i> cf. <i>liguricus</i>
Platanaceae	<i>Platanus</i>		<i>Platanus leucophylla</i>
Polygonaceae	<i>Rumex</i>		
Ranunculaceae		(cf. <i>Batrachium</i> sp.)	
Rhamnaceae	Rhamnaceae		
Rosaceae	(Rosaceae)	( <i>Rubus</i> sp.)	<i>Rosa</i> sp.
Rubiaceae		( <i>Cephalanthus</i> sp.)	
Rutaceae	(Rutaceae)	( <i>Toddalia maii</i> )	
		( <i>Zanthoxylum</i> sp.)	
Salicaceae	<i>Salix</i>		( <i>Salix varians</i> vel <i>S. holzeri</i> )
Scrophulariaceae		( <i>Paulownia cantalensis</i> )	
Solanaceae		(Solanaceae)	
		( <i>Solanum</i> sp.)	
Sterculiaceae	( <i>Reevesia</i> )		
Styracaceae	Styracaceae		
Symplocaceae			<i>Symplocos rara</i>
Theaceae		( <i>Eurya stigmosa</i> )	<i>Gordonia emanuelii</i>
			<i>Gordonia pannonica</i>
			<i>Gordonia styriaca</i>
			<i>Schima mataschensis</i>
Tiliaceae	Tiliaceae		
Trapaceae	( <i>Trapa</i> )	( <i>Trapa silesiaca</i> )	
Ulmaceae	<i>Ulmus</i>		<i>Ulmus carpinooides</i>
	<i>Celtis</i>		
	( <i>Zelkova</i> )		
Umbelliferae		( <i>Umbelliferopsis molassicus</i> )	
Urticaceae	Urticaceae		
Violaceae		( <i>Viola</i> aff. <i>neogenicus</i> )	

Table 2. Continued

Family	Pollen record	Fruit record	Leaf record
Viscaceae		( <i>Viscum</i> sp.)	<i>Viscum morlotii</i>
Vitaceae	<i>Parthenocissus</i>		
	<i>Vitis</i>	(Vitaceae)	
Fam.indet. (Dicotyledoneae)			cf. <i>Dicotylophyllum dieteri</i>
			( <i>Dicotylophyllum</i> sp.)
Alismataceae		( <i>Caldesia</i> sp.)	
Araceae		( <i>Epipremnites</i> sp.)	
		<i>Urospathites dalgasii</i>	
		( <i>Urospathites</i> sp.)	
Butomaceae		( <i>Butomus</i> sp.)	
Cyperaceae		( <i>Carex</i> sp.)	
		<i>Cladium oligovascularis</i>	
		( <i>Cladium</i> sp.)	
	(Cyperaceae)	(Cyperaceae)	
Hydrocharitaceae		( <i>Stratiotes kaltennordheimensis</i> )	
Lemnaceae vel Araceae		( <i>Lemna</i> vel <i>Lemnospermum</i> sp.)	
Lemnaceae vel Stemonaceae		( <i>Lemna</i> vel <i>Spirellea</i> sp.)	
Poaceae	Poaceae		
Potamogetonaceae		( <i>Potamogeton dubnanensis</i> )	
		( <i>Potamogeton</i> sp.)	
Smilacaceae			<i>Smilax</i> cf. <i>protolanceaeifolia</i>
Sparganiaceae	<i>Sparganium</i>	<i>Sparganium</i> spp.	
Zingiberaceae		( <i>Spirematospermum wetzleri</i> )	
? Zingiberaceae			(? <i>Zingiberoideophyllum liblarensis</i> )
			( <i>Rhizocaulon</i> sp.)

a single specimen only: *Carya*, *Liquidambar*, and *Paulownia cantalensis*.

Among the few taxa in the fruit record that may be interpreted as representatives of zonal vegetation, *Fagus*, Lauraceae, and Theaceae agree with the leaf record. Among those that may represent either azonal or zonal taxa or solely azonal ones, the fruit and leaf record share *Alnus*, *Magnolia*, and *Myrica*.

The pollen samples P1-P20 from the sedimentary sequence between the lower and the upper leaf-bearing horizons (Fig. 3) are rather poor, except for samples P8b and P9, which resemble the spectra of P23b (base of the sequence) and P21 (upper leaf-bearing level), although P8b differs by the presence of *Mastixia*, P9 by a higher percentage of pine pollen grains, and P8b and P9 by somewhat higher percentages of *Engelhardia*.

Contrary to the leaf and pollen record from the interval 25–26.5 m, the diaspore spectrum from sample D12 is extremely poor, yielding a single woody taxon (*Carpinus*) and three hydro-helophytes (*Urospathites dalgasii*

(Hartz) Gregor & Bogner, *Cladium oligovascularis* Mai in Knobloch, and *Sparganium*), respectively. Among the pollen samples, sample P21 (upper leaf-bearing sediments) is the richest. Most taxa present in sample P21 also occur in sample P23b (base of the profile) except for Hamamelidaceae, *Ilex*, *Lonicera*, *Reevesia*, and *Zelkova*, which are present in the latter but absent from the former. The pollen and leaf record of this level share the following taxa: *Acer*, *Alnus*, *Betula*, *Buxus*, *Fagus*, *Myrica*, *Nyssa*, *Quercus*, *Platanus*, *Trigonobalanopsis*, and *Ulmus*. Sample P21 also bears higher percentages of *Abies*, *Cathaya*, *Picea*, and *Tsuga*, and vice versa, lower values of Cupressaceae (former Taxodiaceae) pollen than the samples from the sediment succession below. This points to an increased allochthonous impact in the upper part of the section.

The fruit and pollen records indicate a facial change from swampy, lacustrine environment with marshes, ponds, and *Glyptostrobus*-dominated swamp forests at the base of the Feldbach Formation to more diversified fluvial

environments at its top. The strong contrasts in composition, diversity, and species abundances between the basal and the hanging leaf assemblage confirm this interpretation, but document only the initial species-poor *Glyptostrobus*-rich swampy stage and the final species diverse phase at the top of the section because the sediments in between lack leaf remains. However, when comparing the leaf assemblage of the interval 25–26.5 m to the fruit and pollen record of the sediments below (interval 0–25 m), note that the time frame represented in the sedimentary succession may comprise less than several million years, although the exact period is still unclear.

Summarizing, the results obtained from the different organ assemblages are complementary, but only the here-described leaf assemblage provides new and surprising insights into the Pannonian floristic record of the Paratethys region. The fruit record is probably taphonomically strongly biased in so far as azonal taxa account for more than 50% of all taxa (see below) and larger-sized diaspore taxa are rare and, if present, documented by single specimens only (e.g. one remain of *Carya*). Thus, the rather low species diversity and scarcity of zonal taxa with larger-sized diaspores can be explained. Hofmann (Meller & Hofmann 2004) states that the pollen spectrum from Mataschen does not differ from other early late Miocene pollen spectra known from Austria. With very low percentages, *Ilex*, *Mastixia*, *Reevesia*, and Rutaceae are documented from Mataschen. But taxa characteristic of pollen spectra of the “Younger Mastixioid” type such as Rutaceae, Sapotaceae, *Symplocos* or Theaceae are not available from the pollen record.

#### ZONAL VEGETATION INTERPRETATION

Recently, a semi-quantitative method has been developed to interpret the fossil plant record in terms of zonal vegetation. Described in detail by Kovar-Eder & Kvaček (2003, submit.) and Kovar-Eder et al. (submit.), it is based on a primarily taxonomic / physiognomic grouping, reflecting additionally major sociological components recognisable in the fossil record. Among others, this method is advantageous because, based primarily on

taxonomy, leaf taxa of problematic systematic affinity can be assigned by physiognomic features. Every taxon of a respective flora has the value one and is assigned to one or more components, in the latter case the value one is split (Tabs 3–5). Separating azonal from zonal taxa, this grouping scheme enables reasonably objective comparability between the different fossil organ assemblages (leaf, fruit, pollen), which undergo different taphonomic processes before becoming fossilized. Zonal taxa comprise the CONIFER, BLD (broad-leaved deciduous), BLE (broad-leaved evergreen), SCL (sclerophyllous), LEG (legume-type) PALM components, and ZONAL HERB (DRY HERB + MESOPHYTIC HERB) components. Azonal taxa comprise the AZONAL WOODY, AZONAL HERB, FERN, and AQUATIC components.

Vegetation formations have been defined based on the proportions of zonal woody angiosperms (i.e. proportions of the BLD, BLE, and SCL+LEG components respectively of the BLD+BLE+SCL+LEG+PALM components) and the proportion of zonal herbs (MESOPHYTIC HERB + DRY HERB component) of all zonal taxa (CONIFER+BLD+BLE+SCL+LEG+PALM+ MESOPHYTIC HERB + DRY HERB components). These proportions are indicative of the degree of forest desintegration and spreading of open vegetation (Kovar-Eder & Kvaček submit., Kovar-Eder et al. submit.).

For the validation of this recently developed method, plant localities yielding different well-studied organ assemblages like Mataschen are most relevant. First, the different organ assemblages (leaves, fruits pollen) are evaluated separately as described above (Tabs 4–5). This step is followed by a joint evaluation from which the respective zonal vegetation formation is finally derived (Tab. 6).

For Mataschen, the spectra of all investigated samples of the respective organ assemblages were evaluated jointly: the leaf samples from the bottom and the top of the sequence in Table 3, all diaspore samples in Table 4, all pollen samples in Table 5. The fusion of the samples from the bottom to the top of the sequence at Mataschen is justified because the diaspore spectra of the single samples are rather poor, biasing a separate evaluation. Moreover, the time interval included in this sediment sequence is probably stratigraphically minor.



Table 3. Continued

1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
<i>Quercus rhenanasimilis</i>			1.00												1
<i>Rosa</i> sp.		1.00													1
<i>Salix holzeri</i> vel <i>varians</i> <sup>1)</sup>													1.00		1
<i>Schima mataschensis</i>			1.00												1
<i>Smilax</i> cf. <i>protolanceaeifolia</i>			1.00												1
<i>Symplocos rara</i>			1.00												1
<i>Trigonobalanopsis rhamnoides</i>			1.00												1
<i>Ulmus carpinoides</i>		0.25											0.75		1
<i>Viscum morlotii</i>														1.00	1
? <i>Zingiberoideophyllum liblar-ense</i> <sup>1)</sup>								1.00							1
sum of leaf taxa	0.00	8.33	16.33	1.50	1.00	2.50	0.00	2.00	0.00	1.00	0.00	0.00	9.83	2.00	42
sum of zonal leaf taxa <sup>6)</sup>															27
sum of zonal woody angiosperms (leaves) <sup>2)</sup>															27
single components percentage of zonal woody angiosperms <sup>3)-5)</sup>		30.7	60.1	5.5	3.7	9.2	0								100
percentage of zonal herbs of zonal taxa <sup>7)</sup>											0	0			0

Not surprisingly, the pollen record is the richest in taxa (93), followed by the fruit record (64) and the leaf record (42). The number of zonal taxa is almost identical in the leaf and diaspore spectra (27 taxa) and make up 55 taxa in the pollen record; zonal taxa therefore account for 64% in the leaf, 42% in the fruit, and 59% in the pollen record. Vice versa, the fruit and the pollen record yield distinctly higher proportions of azonal taxa (34 taxa / 53% and 38 taxa / 41%, respectively) than the leaf record (13 taxa / 31%). The BLE component of zonal woody angiosperms is richest in the leaf assemblage, both numerically (16 leaf, 7 fruit, 10 pollen taxa) and proportionally (leaves 60%, fruits 33%, pollen 27%). In fact, these relations among different organ assemblages at one site – namely the high diversity of zonal taxa in the leaf record compared to the fruit and pollen record as well as the higher diversity of broad-leaved evergreen taxa in the leaf than in the fruit and pollen assemblages – are rather unusual. This clearly distinguishes the flora from Mataschen from other Neogene floras. The BLD component of zonal woody angiosperms is represented almost complementarily to the BLE component (leaf 31%, fruit 61%, pollen 59%) because the LEG + SCL components of zonal woody angiosperms never reach 10% in any of the different organ floras. In the fruit and the pollen spectra, the ZONAL HERB component of all zonal taxa reaches 18% and 17% respectively. While being almost

equally represented in the pollen record (9/8%), the DRY HERB component reaches almost 3% and the MESOPHYTIC HERB component 16% in the diaspore spectrum. According to the classification of zonal vegetation (Kovar-Eder et al. submit.) the separate evaluation of the different organ spectra from Mataschen yields a “zonal subtropical broad-leaved evergreen forest” based on the leaf and the fruit record (BLE component of zonal woody angiosperms  $\geq 30\%$ , SCL+LEG components  $< BLE$  component of zonal woody angiosperms, zonal herbs  $< 25\%$  of all zonal taxa) and a “zonal warm-temperate to subtropical mixed mesophytic forest” based on the pollen spectrum (BLE component of zonal woody angiosperms  $< 30\%$ , BLD component  $< 80\%$ , SCL+LEG components  $< 20\%$ , zonal herbs  $< 30\%$  of all zonal taxa). For the pollen record, the investigations by Kovar et al. (submit.) and Kovar-Eder & Kvaček (in prep.), which focused on plant sites with different, well-evaluated organ assemblages, demonstrate that the pollen spectra more often indicate vegetation formations that require slightly more intermediate conditions than indicated by the leaf and diaspore record. This is because many taxa of the pollen record are determined either to the family or the generic but hardly ever to a deeper taxonomic level. In addition, the pollen record often still includes far-distance influence.

In the following joint evaluation of the leaf, fruit, and pollen record from Mataschen, the

**Table 4.** Evaluation of the fruit record including the floristic spectra of all diaspore samples from the outcrop in Mataschen (Meller & Hoffman 2004) to determine main vegetation features and zonal vegetation formation. Legend as for Table 3

Vegetation components Taxon	CONIFER component	BLD component	BLE component	SCL component	LEG component	SC+LEG component	PALM component	AZONAL HERB component	AQUATIC component	FERN component	DRY HERB component	MESOPHYTIC HERB component	AZONAL WOODY component	count/ excl	sum
1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
<i>Actinidia</i> sp.		0.50											0.50		1
cf. <i>Ajuga</i> sp.												1.00			1
<i>Alnus</i> sp.		0.50											0.50		1
Araliaceae		0.33	0.33										0.33		1
<i>Batrachium</i> sp.									1.00						1
<i>Broussonetia</i> sp.		1.00													1
<i>Butomus</i> sp.									1.00						1
<i>Caldesia</i> sp.									1.00						1
<i>Carex</i> sp.								1.00							1
<i>Carpinus</i> sp.		1.00													1
<i>Carya</i> sp.		0.50											0.50		1
<i>Cephalanthus</i> sp.													1.00		1
<i>Ceratophyllum</i> sp.									1.00						1
<i>Cladium oligovasculare</i>								1.00							1
<i>Cladium</i> sp.								1.00							1
<i>Corylus</i> sp.		0.50											0.50		1
Cyperaceae								1.00							1
<i>Decodon globosus</i>								1.00							1
<i>Decodon</i> sp.								1.00							1
cf. <i>Eoeryale</i> sp.									1.00						1
<i>Epipremnites</i> sp.												1.00			1
cf. Ericaceae		0.25	0.25	0.25									0.25		1
Euphorbiaceae		0.30	0.60	0.60							0.60	0.60	0.30		3
<i>Eurya stigmosa</i>			1.00												1
<i>Fagus deucalionis</i>		1.00													1
<i>Ficus potentilloides</i>			1.00												1
<i>Glyptostrobus europaeus</i>													1.00		1
cf. <i>Hypericum holyi</i> vel <i>Carpolithes dorofeevii</i>														1.00	1
cf. Lauraceae			1.00												1
cf. <i>Lemna</i> sp.									1.00						1
<i>Lemna</i> sp. vel <i>Spirellea</i> sp.									1.00						1
<i>Liquidambar</i> sp.		0.50											0.50		1
<i>Liriodendron geminata</i>		1.00													1
<i>Magnolia</i> sp.		0.33	0.33										0.33		1
<i>Microdiptera</i> sp.									1.00						1
Moraceae		0.33	0.33										0.33		1
Moraceae vel Ranunculaceae														1.00	1
<i>Myrica</i> sp.		0.33	0.33										0.33		1
<i>Nymphaea</i> sp.									1.00						1
<i>Paulownia cantalensis</i>		1.00													1
<i>Potamogeton dubnanensis</i>									1.00						1
<i>Potamogeton</i> sp.									1.00						1
<i>Proserpinaca</i> sp.									1.00						1
<i>Rubus</i> sp.		0.50	0.50												1
<i>Sambucus</i> sp.		0.50											0.50		1
<i>Selaginella</i> sp.										1.00					1
<i>Sinomenium cantalense</i>		1.00													1
Solanaceae		0.25						0.25				0.25	0.25		1

Table 4. Continued

1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
<i>Solanum</i> sp.								0.50				0.50			1
<i>Sparganium</i> sp.									1.00						1
<i>Spirematospermum wetzleri</i>								1.00							1
<i>Stratiotes kaltennordheimensis</i>									1.00						1
<i>Swida</i> sp.		1.00													1
<i>Toddalia maii</i>			1.00												1
<i>Trapa silesiaca</i>									1.00						1
<i>Umbelliferopsis molassicus</i>														1.00	1
<i>Urospathites dalgasii</i>								1.00							1
<i>Urospathites</i> sp.								1.00							1
aff. <i>Viola neogenica</i>								0.50				0.50			1
cf. <i>Viola</i> sp.								0.50			0.10	0.40			1
Vitaceae		0.50	0.25										0.25		1
<i>Zanthoxylum</i> sp.		0.33	0.33	0.33											1
sum of fruit taxa	0.00	13.45	7.25	1.18	0.00	1.18	0.00	10.75	14.00	1.00	0.70	4.25	7.37	3.00	64
sum of all zonal fruit taxa <sup>6)</sup>															27
sum of zonal woody angiosperms (fruits) <sup>2)</sup>															22
single component's percentage of zonal woody angiosperms <sup>3)-5)</sup>		61.5	33.1	5.4	0	5.4	0								100
percentage of zonal herbs of zonal taxa <sup>7)</sup>											2.6	15.8			18

numbers of taxa of the respective components are added and the proportions of the different components are calculated in the same way as described above for the individual organ assemblages (Tab. 6). The proportion of the BLE component of zonal woody angiosperms reaches 39%, the BLD component 51%, the SCL+LEG components 10%, and the ZONAL HERB component of all zonal taxa 13%. The thus derived most likely zonal vegetation unit for the Mataschen floristic record is the “zonal subtropical broad-leaved evergreen forest”. In this context, note that in pollen and fruit assemblages which are to be assigned to this unit due to their high BLE component ( $\geq 30\%$ ), the low percentage of zonal herb taxa seems to be reflected in the fossil record (Kovar-Eder et al. submit.). In modern forest vegetation, largely evergreen canopy and shrub layer account for a poor angiospermous ground cover. Additional fossil plant sites with different well-studied organ assemblages are required to test whether this observation in the currently available fossil floras can be validated or whether it is a mere artefact.

Returning to the floristic composition of the leaf assemblage from the top of the sequence in Mataschen, most of the recorded species cannot be correlated one-to-one to modern species. In most cases, the correlation remains at the generic or even only family level (Lauraceae).

However, the composition of this assemblage – with 5 Lauraceae, 2 evergreen Fagaceae, 4 Theaceae, *Symplocos*, cf. *Distylium*, and *Magnolia* alongside several more, partly so far unknown, probably evergreen taxa – points solely to a comparison with largely broad-leaved evergreen forest regions of South-east Asia.

“Evergreen broad-leaved forests of evergreen oaks, *Schima*, and laurels” thrive in southern parts of China, Vietnam, Siam, Burma, southern parts of Japan, and on Taiwan, showing rather large regional variability (Wang 1961). Among the evergreen broad-leaved forest formation, Wang further discriminates three forest types. Of these, the “evergreen sclerophyllous broad-leaved forest” in ecotonal regions (there with *Fagus*) and in regions where lauraceous taxa are more prominent than evergreen Fagaceae seems best comparable to the fossil record from Mataschen. Generally, evergreen oaks (*Quercus*, *Castanopsis*, *Lithocarpus* incl. former *Pasania*) are very diverse in this forest type but appear mostly in mixed communities with various proportions of Theaceae, Lauraceae, Magnoliaceae, and Hamamelidaceae. In tree constituents, this forest type is at least as rich as the mixed mesophytic forest type. In southern maritime regions of China, in Japan, and on Taiwan these forests are also known as oak-laurel forests (Chaney & Chuang 1968).

**Table 5.** Evaluation of the pollen record including the floristic spectra of all pollen samples from the outcrop in Mataschen (Meller & Hofmann 2004) to determine main vegetation features and zonal vegetation formation. Legend as for Table 3

Taxon	Vegetation components														count/ excl	sum
	CONIFER component	BLD component	BLE component	SCL component	LEG component	SC+LEG component	PALM component	AZONAL HERB component	AQUATIC component	FERN component	DRY HERB component	MESOPHYTIC HERB component	AZONAL WOODY component			
1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	
<i>Abies</i>	1.00														1	
<i>Acer</i>		1.50											0.50		2	
<i>Alnus</i>		1.00											1.00		2	
Araliaceae		0.50	0.30										0.20		1	
<i>Artemisia</i>											1.00				1	
Asteraceae								0.66			0.66	0.66			2	
<i>Betula</i>		0.50											0.50		1	
<i>Buxus</i>			0.50	0.50											1	
<i>Calystegia</i>								0.20			0.40	0.40			1	
<i>Carpinus</i>		1.00													1	
<i>Carya</i>		1.00											1.00		2	
Caryophyllaceae								0.20			0.60	0.20			1	
<i>Castanea vel Lithocarpus</i>		0.50	0.50												1	
<i>Cathaya</i>	1.00														1	
<i>Cedrus</i>	1.00														1	
<i>Celtis</i>		0.50		0.50											1	
<i>Cercidiphyllum</i>		0.50											0.50		1	
Chenopodiaceae								0.25			0.50	0.25			1	
<i>Cornus</i>		1.00													1	
Cupressaceae	1.00												1.00		2	
Cyperaceae								1.00				1.00			2	
<i>Decodon</i>								1.00							1	
Empetraceae													1.00		1	
<i>Engelhardia</i>		1.00	1.00												2	
Ericaceae		0.50	0.50	0.50									0.50		2	
<i>Fagus</i>		1.00													1	
<i>Fraxinus</i>		0.50											0.50		1	
Hamamelidaceae		0.75	0.25												1	
<i>Ilex</i>		0.50	0.50	0.50									0.50		2	
<i>Juglans</i>		1.00													1	
<i>Liquidambar</i>		0.50											0.50		1	
<i>Lonicera</i>		0.25	0.25	0.25									0.25		1	
<i>Lycopodium</i>										1.00					1	
<i>Mastixia</i>			1.00												1	
<i>Myrica</i>		0.66	0.66										0.66		2	
<i>Myriophyllum</i>									1.00						1	
Myrtaceae			0.50	0.50											1	
<i>Nyssa</i>		0.50											0.50		1	
<i>Osmunda</i>										1.00					1	
<i>Parthenocissus</i>		0.80	0.20												1	
<i>Picea</i>	1.00														1	
<i>Pinus</i>	1.50												0.50		2	
<i>Platanus</i>		0.50											0.50		1	
Poaceae								0.66			0.66	0.66			2	

Table 5. Continued

1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Polypodiaceae										5.00					5
Pteridaceae										2.00					2
Pteridophyta										5.00					5
<i>Pterocarya</i>		0.50											0.50		1
<i>Quercus</i>		0.75	0.75	0.75									0.75		3
<i>Reevesia</i>			1.00												1
Rhamnaceae		0.25	0.25	0.25									0.25		1
Rosaceae		0.50									0.50	0.50	0.50		2
<i>Rumex</i>								0.30			0.20	0.50			1
Rutaceae		0.25	0.25	0.25									0.25		1
<i>Salix</i>													1.00		1
<i>Sciadopitys</i>	0.50												0.50		1
<i>Selaginella</i>										0.50		0.50			1
<i>Sparganium</i>								1.00							1
Styracaceae		0.50	0.50												1
Tiliaceae		1.50											0.50		2
<i>Trapa</i>									1.00						1
<i>Trigonobalanopsis</i>			1.00												1
<i>Tsuga</i>	1.00														1
<i>Ulmus</i>		0.66		0.66									0.66		2
Urticaceae		0.33									0.33		0.33		1
<i>Vitis</i>		0.50											0.50		1
<i>Zelkova</i>		0.33		0.33									0.33		1
sum of pollen taxa	8.00	22.53	9.91	4.99	0.00	4.99	0.00	5.27	2.00	14.50	4.85	4.67	16.18	0.00	93
sum of zonal pollen taxa <sup>6)</sup>															55
sum of zonal woody angiosperms (pollen) <sup>2)</sup>															37
single component's percentage of zonal woody angiosperms <sup>3)-5)</sup>		60.2	26.5	13.3	0	13.3	0								100
percentage of zonal herbs of zonal taxa <sup>7)</sup>											8.8	8.5			17

Table 6 Joint evaluation of the leaf, fruit, and pollen record from Mataschen to determine main vegetation features and zonal vegetation formation. Legend as for Table 3

Joint evaluation of the leaf, fruit, and pollen record	CONIFER component	BLD component	BLE component	SCL component	LEG component	SCL+LEG component	PALM component	AZONAL HERB component	AQUATIC component	FERN component	DRY HERB component	MESOPHYTIC HERB component	AZONAL WOODY component	Count/ excl	Sum of all taxa	Sum of all zonal taxa <sup>6)</sup>	Sum of zonal woody angiosperms <sup>2)</sup>
Leaf record	0.00	8.33	16.33	1.50	1.00	2.50	0.00	2.00	0.00	1.00	0.00	0.00	9.83	2.00	42	27	27
Fruit record	0.00	13.45	7.25	1.18	0.00	1.18	0.00	10.75	15.00	1.00	0.70	4.25	7.37	3.00	64	27	22
Pollen record	8.00	21.78	9.91	4.99	0.00	4.99	0.00	5.27	2.00	14.50	4.85	4.67	16.43	0.00	93	54	37
Sum of leaf, fruit, and pollen taxa	8.00	44.56	33.49	7.67	1.00	8.67	0.00	18.02	16.00	16.50	5.55	8.92	33.63	5.00	199	109	87
Single components percentage of zonal woody angiosperms <sup>3)-5)</sup>		51.2	38.7	8.8	1.2	10.0	0							100			
Percentage of zonal herbs of zonal taxa <sup>7)</sup>										5.1	8.2						

## CLIMATIC IMPLICATIONS

The climatic conditions under which the vegetation around Mataschen thrived are best derived from the distribution area of comparable modern vegetation, i.e. the “evergreen sclerophyllous broad-leaved forest” sensu Wang (1961). Taking into account six regions at different longitudes/latitudes and altitudes to cover the large distribution region of this forest formation, the following climatic parameters can be deduced for these forests today (Wang 1961): mean (M) annual temperature (T) 15.4–19.3°C, MT of the coldest month (January) 5.3–9.5°C, MT of the warmest month (July/August) 20.4–29°C, no. of months with MT below 0°C: 0, no. of months with extreme minimum T below 0°: 4–5, extreme minimum T: –6.7 to –3.7°, no. of months with MT above 22°: 0 and 5–6, extreme maximum T: 30.5–47.2°C, no. of months with MT > 10 °C: 9–11, M annual precipitation (P): 1284 mm–1947 mm, P of wettest 3 months: 41.9–69.5% of total, P of the driest 6 months: 10.4–26.6% of total, MP of the driest month: 4.7–43.5 mm. Within the geographical range of the “evergreen sclerophyllous broad-leaved forest”, climate diagrams (Walter & Lieth 1967) are scarcely available. The climate diagram for Tengyueh and the data for Tengchung (Yunnan), which are probably synonymous (Wang 1961, tab. 14, based on the years 1943–45), are fairly consistent.

Concluding from the presence of deciduous taxa such as *Fagus* and cf. *Betula* characteristic of the ecotone of the evergreen broad-leaved forest formation towards mixed mesophytic forests, lower and middle values for the temperature regime are more likely than maximal temperature values; for precipitation, middle to higher values within the given range are more probable.

THE FLORA OF MATASCHEN  
COMPARED TO THE MIDDLE MIOCENE  
TO EARLY PLIOCENE PLANT RECORD  
OF HUNGARY

The location of Mataschen at the western margin of the Pannonian Basin (i.e. the eastern Styrian Basin) calls for detailed comparison with the rich Hungarian Neogene plant record.

After Hably (1985) Badenian floras are known from NE Hungary: Eger-Tihamér, Gyöngyöspata, Hont, Sajómercse, Szurdokpüspöki (early Badenian), and Nógrádszakál (early and late Badenian). Most of these localities are characterized by the presence of Lauraceae, above all of *Daphnogene*, thus showing a relationship to the flora of Mataschen. Moreover, Mataschen and the Hungarian floras of the Badenian share the presence of *Glyptostrobus europaeus* and *Myrica lignitum*, swamp elements widely distributed in space and time.

Sarmatian plant assemblages have been recorded from the northeastern part of Hungary. These localities share with Mataschen *Glyptostrobus europaeus*, *Daphnogene* sp., *Platanus leucophylla*, *Quercus kubinyii*, *Fagus*, *Alnus*, *Acer tricuspidatum*, *Rosa*, *Myrica*, and *Nyssa* (Hably 1985, Erdei & Hír 2002). The flora of Sopron-Piusz Puszta (Western Hungary) deserves attention because it yields dispersed, organically preserved plant material appropriate for cuticular studies (Erdei 1996, Erdei & Lesiak 1999–2000). As at Mataschen, this plant assemblage comprises *Buxus pliocenica*, *Laurophyllum pseudoprinceps*, further unidentified *Laurophyllum* species, *Magnolia liblarensis*, and *Viscophyllum* sp., which may be related to *Viscum morlotii*.

The rich and thermophilous Sarmatian flora and vegetation that thrived in the Pannonian Basin withdrew from most parts of the basin during the Pannonian and was replaced by species-poor wetland vegetation. Nonetheless, zonal vegetation survived on “inselbergs” and in the marginal areas, as proved by fossil plant remains recorded from such areas (Hably 2003; Neuhaus am Klausenbach, Pannonian Basin, Burgenland, Austria close to the Hungarian border, Kovar-Eder et al. 1995; Rudabánya, Kretzoi et al. 1976). Favourable depositional conditions in the Pannonian Basin account for the high number of plant sites, most of which represent wetland environments. We restrict our comparisons to more thoroughly investigated floras (Iharosberény-I and Tiszapalkonya-I Boreholes, Tihany-Fehérpart, Dozmat, Rudabánya, Sótöny, Balatonszentgyörgy Hably 1992a, b, c, Hably & Kovar-Eder 1996, Hably 2003, Horváth 1961, Kretzoi et al. 1976, Pálfalvy 1977). Previously, the age of most of these localities was ambiguous, often cited as Pliocene (Horváth 1961, 1963, 1964, 1971–72,

Pálfalvy 1977), but Magyar and Hably (1994) demonstrated them to be more likely of late Miocene age.

Some plant-bearing localities, like Balatonszentgyörgy and Rózsaszentmárton, have been correlated to the *Congeria balatonica-Lymnocardium decorum* zone (Bartha & Soós 1955) based on the occurrence of characteristic brackish molluscs in the layers overlying the plant-bearing beds. According to the mammal stratigraphic, radiometric, and palaeomagnetic evidence, this zone is older than 7.5 and younger than 8.5 Ma (Müller & Magyar 1992). Recently, new collections were studied from this area, and *Prosodacnomya* was identified, which was yet unknown from this region. This occurrence is unique because *Prosodacnomya* co-occurs here sometimes with either *Lymnocardium decorum* or *L. serbicum*, which is exceptional. The separate occurrences of these taxa were used to differentiate the biozones. Their co-occurrence confirms that they belong to the biozone *Lymnocardium serbicum* – *Prosodacnomya carbonifera*, which is dated to about 8 million years (Sztano et al. 2005).

Several localities lack stratigraphically relevant information, including Sé, Sótony, Kemenesmihályfa, and several others in the Vas county (West Hungary). They are considered to be of late Miocene age because Pliocene age in surface exposures is restricted to maar deposits (alginites). The Baltavár mammal fauna that derives from this region is of Messinian age (Magyar & Hably 1994) and the fossil-bearing beds are overlain by Holocene sediments there.

The age of the deposits at Rudabánya has been revised to  $11.4 \pm 0.1$  m.a., i.e. latest Sarmatian/early Pannonian based on a single crystal argon date and latest MN 9 (i.e. ca. 10–9.7 m.a., middle Pannonian) based on biochronological correlations (Bernor et al. 2003).

The former geographic position of Rudabánya at the margin of the Pannonian Basin may account for a relatively higher number of zonal elements in this flora than in other plant assemblages from the Pannonian Basin of comparable age. Among these, thermophilous taxa are remarkable, e.g. *Daphnogene*, *Sassafras*, and *Engelhardia macroptera*. Nevertheless, the flora of Rudabánya shares with Mataschen only few taxa: *Glyptostrobus europaeus*, *Alnus menzelii*, Betulaceae, *Daphnogene*, and *Fagus*.

Rudabánya bears also *Nyssa*, *Ulmus*, *Quercus*, *Myrica*, and *Acer*, but these taxa differ at the species level.

Most of the other Pannonian floras document rather species-poor wetland (mainly swampy) environments. In these assemblages, *Glyptostrobus europaeus*, *Byttneriophyllum tiliifolium* (Al. Braun) Knobloch & Kvaček, and *Alnus cecropiifolia* (Ettingshausen) Berger are the main components, often occurring mass-wise, thus documenting a most characteristic type of swamp vegetation (Hably 2003). Although the plant assemblage from the base of the exposure in Mataschen represents a swampy *Glyptostrobus*-dominated habitat, neither *Byttneriophyllum tiliifolium* nor *Alnus cecropiifolia* have been recorded there. Instead, mass occurrences of leaves of reed-like monocotyledons, fruits of *Spirematospermum wetzleri* (Heer) Chandler, the fern "*Pteris*" *oeningensis* Unger, *Juglans acuminata* Al. Braun ex Unger, *Myrica*, and *Salix* have been recorded alongside *Trapa silesiaca* Göppert, documenting the diversity of swampy habitats in the Pannonian realm. At Hungarian plant sites representing riparian environments, *Alnus ducalis* (Gaudin) Knobloch, *Alnus gaudinii* (Heer) Knobloch & Kvaček, *Liquidambar europaea* Al. Braun, *Platanus leucophylla*, *Populus* div. sp., and *Salix* sp. are important elements (Hably 1992b). Except for *Platanus leucophylla* and *Alnus* sp., none of them is documented from Mataschen. Betulaceae, *Ulmus carpinooides*, and *Fagus* sp. – rare elements in the Hungarian Pannonian – are rather well represented at Mataschen. The flora of Aranyosgadány (Mecsek Mts., Hably 1999 manuscript), which represents an "inselberg", includes the only record of *Quercus kubinyii* from the Hungarian Pannonian. Rarely occurring taxa at Hungarian sites that are also documented from Mataschen are *Acer*, *Quercus* (Horváth 1971–72), and *Smilax* (Hably 1992b).

Well-dated Pliocene floras are known from volcanic areas of Western Hungary. The floras of Gérce and Pula excavated from alginite layers in the infill of crater lakes have been quite thoroughly investigated (Kvaček et al. 1994, Hably et al. 1996, Hably & Kvaček 1997). These fossil plant assemblages, which strongly reflect hinterland vegetation, share with Mataschen the presence of *Buxus pliocenica* and *Quercus kubinyii*. One specimen each

of *Magnolia* sp. and *Rosa* sp. are also noteworthy from Gércse because these taxa have been recorded from Mataschen as well.

The Pliocene floras provide evidence for the survival of the impoverished Sarmatian flora in the Pannonian region. A decrease in diversity is proved by the absence of thermophilous species, e.g. *Tetraclinis*, Lauraceae, *Podocarpium podocarpum* (A. Br.) Herendeen, *Berberis andreanszkyi* Z. Kvaček & Erdei, *Quercus mediterranea* Unger, *Sapindus falcifolius* Al. Br., *Ailanthus confucii* Unger, *Pistacia lentiscoides* Unger, *Ilex parschlugiana* Unger, *Toddalia* sp., *Koelreuteria macroptera* (Kováts) Edwards, *Sabalites* sp.. The appearance of new taxa *Tsuga* sp., *Juniperus* sp., *Torreya* sp., *Sassafras ferretianum* Massalongo & Scarabelli, *Eucommia* sp., *Crataegus* sp., *Ribes* sp., *Acer pseudomonspessulanum* Unger, and *Ampelopsis cf. malvaeformis* (Schlotheim) Mai indicate further floristic change (Hably 2003).

Generally, the Sarmatian plant record more closely resembles the flora of Mataschen than the Pannonian one, except for Rudabánya. These differences may be partly caused by different facies that are represented in the Pannonian record, i.e. the assemblage from the base in Mataschen – *Glyptostrobus*-reed-rich swamp vegetation, the assemblage from the top in Mataschen – predominantly reflecting the zonal flora, whereas Iharosberény-I, Tiszapalkonya-I Boreholes, Tihany-Fehérpart, Dozmat, Sótöny, and Balatonszentgyörgy predominantly represent *Glyptostrobus-Byttneriophyllum-Alnus cecropiifolia* swampy facies.

Moreover, numerous species recorded from Mataschen require cuticle preservation for determination, but organic preservation of fossil leaves is rare in Hungary. So far unknown from Hungarian floras are *Laurophyllum pseudovillense*, *Laurus abchasica*, “*Quercus*” *rhenanasimilis*, *Trigonobalanopsis rhamnoides*, *Oleinites* cf. *liguricus*, *Gordonia* div. sp., *Schima mataschensis*, *Dicotylophyllum uhudler*, *Symplocos rara*, and *Dicotylophyllum dieteri*. Vice versa, numerous taxa characteristic of the Sarmatian and early Pannonian floras of Hungary were not recorded in Mataschen, e.g. *Ginkgo adiantoides* (Unger) Heer, *Zelkova zelkovifolia* (Unger) Bůžek & Kotlaba, *Ulmus braunii* Heer, *Populus populina* (Brongniart) Knobloch, *Carpinus* div. sp., roburoid oaks, *Acer integerrimum* (Viviani) Massalongo, *Pterocarya paradisiaca* (Unger) Iljinskaja,

*Parrotia pristina* (Ettingshausen) Stur, and “*Diospyros*” *brachysepala* Heer.

## THE FLORA OF MATASCHEN IN THE EUROPEAN FLORISTIC CONTEXT

Only a broad comparison of the European early Miocene to early Pliocene plant record can improve our understanding of the relevance of the here described flora, which is characterized above all by the presence of five species of Lauraceae, four of Theaceae, four of Fagaceae (two of them evergreen ones), of cf. *Dicotylophyllum dieteri*, *D. uhudler* (a probably evergreen Ericaceae), *Oleinites* cf. *liguricus*, *Symplocos rara*, and *Smilax* cf. *protolanceae-folia*. Here, we compare representative floras of the time interval early Miocene to Pliocene focusing on selected stratigraphically and ecologically relevant taxa (Tab. 7).

The early Miocene floras of Saxony, assigned to the “Florenkomplex Brandis” correlated to the early Miocene (Mai & Walther 1991), are not included in Table 7 because essential species listed to occur at single sites lack descriptions in the systematic part (e.g. *Platanus leucophylla* and *Symplociphyllum weylandii*). From the Lower Rhine embayment (Inden Formation) more leaf taphocoenoses are known. We restrict ourselves here to floras offering the possibility of relevant comparison.

The **Lauraceae** are represented by five (Mydlovary complex, southern Bohemia; Knobloch & Kvaček 1996) to eight species (Cypris clay, Bohemia, Bůžek et al. 1996). Mataschen shares with these floras the presence of *Daphnogene polymorpha*, *Laurophyllum pseudoprinceps*, and *Laurus abchasica*, and with Oberdorf (Köflach-Voitsberg lignite area; Kovar-Eder et al. 2001), Hrádek n.N. (North Bohemia, published only partly; Kvaček 1971), and Wackersdorf (Bavaria; Knobloch & Kvaček 1976) also *Laurophyllum pseudovillense*. However, *L. rugatum*, which is present in the Cypris shale, Oberdorf, Hrádek n.N., Wackersdorf, and the Mydlovary complex, along with *L. hradekense*, which is recorded from the Cypris clay, Wackersdorf, Hrádek n.Nisou, and the Mydlovary complex, have not been detected in Mataschen. Regarding the Lauraceae, the Mataschen flora has rather poor relations to floras of late middle Miocene to early Pliocene age from the molasse basin



Table 7. Continued

1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	
Lauraceae	<i>Daphnogene pannonica</i>												X	X		X			X			
	<i>Daphnogene polymorpha</i>	X	X	X	X	X	X	X		X	X							X		X		
	<i>Laurophyllum/Ocotea hradekense</i>	X		X	X	X	X				X									X		
	<i>Laurophyllum markvarticense</i>	X	X					X												X		
	<i>Laurophyllum medimontanum</i>	X																				
	<i>Laurophyllum nechranicense</i>	X																				
	<i>Laurophyllum pseudoprinceps</i>	X	X	X	X	X	X	X	X	X	X		X	cf.				X	cf.	X	X	cf.
	<i>Laurophyllum pseudovillense</i>		X	X	X					X												
	<i>Laurophyllum rugatum</i>	X	X	X	X	X																
	<i>Laurophyllum villense</i>						X															
	<i>Laurus abchasica</i>	X	X	X	X	X	X			X	X											
	Lauraceae gen. et sp. indet.	X					X		X	X			X	X	X	X						
	<i>Sassafras</i> div. sp.	X					X												X	X	X	
Magnoliaceae	<i>Magnolia kristinae</i>	X		X																		
	<i>Magnolia liblarensis</i>		X			X	X		X	X	X							X		X		
Oleaceae	<i>Oleinites liguricus</i>									X	cf.											
Platanaceae	<i>Platanus leucophylla</i>						X			X		X	X	X	X	X	X	X	X	X	X	
	<i>Platanus neptuni</i>	X									X	?										
Salicaceae	<i>Salix</i> div. sp.		X	X		X	X				?	X	X	X	X	X	X	X			X	
	<i>Populus balsamoides</i>					X	X					X						X	X		X	
	<i>Populus populina</i>	X		X		X	X					X	X		X			X	X	X	X	
Symplocaceae	<i>Symplocos rara</i>			X						X												
Theaceae	<i>Gordonia emanuelii</i>									X												
	<i>Gordonia pannonica</i>									X												
	<i>Gordonia styriaca</i>									X												
	? <i>Gordonia oberdorfensis</i>		X																			
	<i>Gordonia hradekensis</i>	X		X																		
	<i>Schima mataschensis</i>									X												
	<i>Ternstroemia sequoioides</i>	X																				
	<i>Ternstroemites waltheri</i>		X																			
	? <i>Cleyera schilcheriana</i>		X																			
	Theaceae gen. et sp. indet.						X															
indet.	<i>Dicotylophyllum dieteri</i>		X			X				X	cf.											
Smilacaceae	<i>Smilax</i> div. sp.	X		X		X	X	X		X	X				X							

(Hausruck/Kobernaussen forest; Kovar-Eder 1988; Kovar-Eder & Wójcicki 2001), Vienna Basin (Vösendorf, Laaerberg; Berger 1952, 1955a, b; Moravska Nova Ves, Knobloch 1969), and Styrian Basin (Wörth/Paldau, Kovar-Eder & Krainer 1990, Krenn 1998). This is partly because Lauraceae (except for *Daphnogene*) are discriminable only by their cuticles, and many of these floras lack cuticle preservation. However, leaves that may be assigned to the Lauraceae based on macro-morphology are generally very scarce in these floras, and even *Daphnogene*, if present at all, is usually rare and its leaves mostly smaller (*Daphno-*

*gene pannonica* Kvaček & Knobloch) than in the early to middle Miocene. Regarding this family, Mataschen shows closer relations to late Miocene/early Pliocene floras of the Lower Rhine embayment (Inden Formation, Belz & Mosbrugger 1994), and certain parts of southern Europe (Romania, e.g. Valeă de Cris; Givulescu 1962, 1975, Northern Italy, Fischer & Butzmann 2002) – regions which already constituted late Miocene/early Pliocene refugia for warmth- and humidity-preferring, mostly evergreen taxa that formerly were widespread across Europe. From the Inden Formation and Valeă de Cris, documented species include

*Daphnogene polymorpha*, *Laurophyllum pseudoprinceps* (cf. from the Inden Formation), and *Laurus abchasica* (as *Cornus graeffii* (Heer) Hantke from the Inden Formation). Cf. *Laurophyllum pseudoprinceps* and *Daphnogene polymorpha* have also been described from Meleto, Northern Italy (Fischer & Butzmann 2002), and *Laurophyllum pseudoprinceps* from Vegora, Greece (Kvaček et al. 2002). There, *Daphnogene polymorpha* is replaced by *D. pannonica*.

*Distylium fergusonii* is often present in floras of the “Younger Mastixioid” type (Cypris clay, Oberdorf, Wackersdorf). To our knowledge, the Mataschen specimen is the most recent record of probable *Distylium* foliage. However, *Distylium* fruits are documented from the late Miocene Inden Formation in the Lower Rhine embayment (van der Burgh 1987), the early Pliocene of the Po Basin (Ca Viettone, Sento, Martinetto et al. 1997); pollen is known from the late Pliocene of the Tiberino Basin (Pontini & Bertini 2000) in Italy.

A further interesting element is *Magnolia liblarensis*, which has been reported from the early Miocene (Oberdorf), the late early/early middle Miocene (Mydlovary Formation, Knobloch & Kvaček 1996; Kreuzau near Düren, Ferguson 1971), and the late middle Miocene (Sopron-Piusz-Pusztá, Western Hungary, Sarmatian, Erdei 1996, Erdei & Hír 2002). Pannonian records are extremely rare and available only from Romania (Valeă de Criș as *Palpilionaceophyllum liblarensis* Kräusel & Weyland; Givulescu 1975) and the Lower Rhine Basin (Inden Formation, described as *Magnolia kristinae* Knobloch & Kvaček, Belz & Mosbrugger 1994). The specimens from Mataschen represent the first Central European late Miocene record, and the youngest one derives from the late Miocene/early Pliocene Mediterranean refuge region (Meleto, Fischer & Butzmann 2002).

Generally, *Symplocos* is extremely rare in the leaf record but diversely represented in diaspore floras and also documented in pollen spectra. It is an essential component of the “Younger Mastixioid” floras. Surprisingly, one leaf fragment with well-preserved cuticle was definitively identified as *Symplocos* in Mataschen. It exactly matches *Dicotylophyllum* sp. 8 from Wackersdorf, for which Kvaček had already suspected the systematic position

within *Symplocos* (Knobloch & Kvaček 1976, Kvaček 2004).

The **Theaceae** record is much more complicated because our understanding of the Neogene diversity of this family is poor. This is evident in the fact that newly described leaf assemblages of the early Miocene/early middle Miocene often include yet unknown Theaceae species. Moreover, numerous species are known only from their type localities. The here described assemblage from Mataschen contains four previously unknown species. This clearly indicates that the monographical treatment of Kvaček & Walther (1984a, b) should be continued to include all the recently described species. The fossil record, however, shows that the Theaceae leaf record is largely restricted to the early and early middle Miocene. Also in this respect, the Pannonian flora of Mataschen resembles floras of this time interval.

We were able to distinguish four species of **Fagaceae** (*Fagus*, *Quercus kubinyii*, “*Quercus*” *rhenanasimilis*, and *Trigonobalanopsis rhamnoides*). Based on the leaf and cuticle texture, the latter two were evergreen, *Q. kubinyii* may be regarded as deciduous or semi-evergreen, and *Fagus*, as in modern beech, was probably deciduous. With the occurrence and abundance of *Trigonobalanopsis rhamnoides*, a further element indicates a close relation of the Mataschen flora to the early and middle Miocene plant record: no further late Miocene record of this taxon is available from northern parts of the Paratethys region. Comparable to the Lauraceae, Theaceae, and *Distylium*, records of *Trigonobalanopsis* (leaves/fruits) are known from late Miocene/early Pliocene refuge habitats such as the Balkan region. This includes Valeă de Criș, Romania, described there as *Castanopsis dechenii* (Weber) Kräusel & Weyland and *Rhamnus rossmässleri* Unger (Givulescu 1962), the Mediterranean, e.g. Ca Viettone, Sento (Martinetto et al. 1997), Meleto (Fischer & Butzmann 2002), and the Lower Rhine Basin, Inden Formation, Pliocene of Brunssum (fruits, van der Burgh 1987, Zagwijn 1990).

The temporal and spatial distribution of “*Quercus*” *rhenanasimilis* remains unclear because this species resembles *Q. rhenana* and may be hidden among records of so-called *Q. rhenana* (see p. 171). However, *Quercus rhenana* is most characteristic of lignite-forming swampy vegetation of the early and early

middle Miocene. We are not aware of any late Miocene record of *Quercus rhenana* or closely resembling taxon. Thus, the record of “*Quercus rhenanasimilis*” in Mataschen, although based on a single leaf fragment only, again indicates closer relations to floras of the older Neogene than to contemporaneous ones from the northern parts of the Central Paratethys region.

Due to the poor preservation, only few leaves can be definitively assigned to *Fagus* (others may be hidden in the group determined as *Betula* vel *Fagus* sp.). Although the species diversity of *Fagus* is open to discussion, the fossil record of beech foliage is a useful tool to discriminate early and late Neogene floras in the Central Paratethys region. Contrary to more northerly regions, unambiguous early Miocene records of *Fagus* foliage are very scarce in the Paratethys region; beech is definitely common from the late middle Miocene onwards. Later, the abundance of beech foliage becomes a characteristic feature of Pannonian leaf assemblages. Moreover, beech was widespread then in Europe, reaching the Mediterranean, e.g. Italy and Greece. The definite presence of *Fagus* in the Lauraceae- and Theaceae-rich plant assemblage of Mataschen distinguishes this flora from compared early/middle Miocene ones.

As *Fagus*, *Platanus leucophylla* is occasionally present in the middle Miocene. In floras from fluvial environments such as Mataschen (e.g. Moravská Nová Ves, Laaerberg), its abundance increases towards the late Miocene. It is absent in the early/early middle Miocene floras of Central Europe, but is present in Kreuzau (Lower Rhine Basin, probably middle Miocene). Thus, the presence and abundance of *Platanus leucophylla* in the Mataschen assemblage constitute further remarkable features of this flora. In this context, note that the record of *P. leucophylla* in the flora of Brandis, “Florenkomplex Brandis”, correlated to the early Miocene (Mai & Walther 1991), is ambiguous (see p. 166).

*Buxus pliocenica* is occasionally present in middle Miocene to Pliocene floras. It has been determined from the middle Miocene of Poland, Stare Gliwice (Szafer 1961, there as *B. sempervirens* L.; Kvaček et al. 1982), Młyny (Zastawniak 1980), and from the Sarmatian of Sopron-Püsz-Pusztá in Western Hungary (Erdei 1996, Erdei & Hír 2002). Its presence in the Sarmatian of Türkenschanze in the Vienna

Basin (Berger & Zabusch 1953) is ambiguous as Kvaček et al. (1982) suspect these remains to represent *Buxus egeriana*. *Buxus pliocenica* is well documented from the early Pliocene of Gerce and Pula in Western Hungary (Fischer & Hably 1991, Hably & Kvaček 1997).

Also remarkable is the record of *Oleinites* cf. *liguricus* because so far *O. liguricus* was known only from the Messinian of the Mediterranean.

The Mataschen assemblage would be expected to contain *Tetraclinis salicornioides* (Unger) Kvaček and *Engelhardia orsbergensis* (Wessel & Weber) Jähnichen, Mai & Walther. We have no explanation for the absence of *Tetraclinis*, whereas *Engelhardia* leaflets are rather soft and probably had a low fossilization potential in this taphocoenosis, which is generally poor in soft-leaved taxa.

In summary, the leaf flora from Mataschen more closely resembles early Miocene to early middle Miocene floras of the “Younger Mastixioid” type sensu Mai of Central Europe than Pannonian floras of the Central Paratethys region. This conclusion is based on species diversity, the composition of mostly laurophyllous taxa, as well as on the abundance of individual taxa. Furthermore, the assemblage from Mataschen is floristically more closely related to late Miocene and early Pliocene floras of southern Europe (Romania, northern Italy, Greece) than to time-equivalent ones of Central Europe. This conclusion is based on the co-occurrence of laurophyllous taxa and (mostly deciduous) taxa characteristic of the middle to late Miocene/Pliocene.

## STRATIGRAPHIC CONSIDERATIONS

Based on the correlation by the brackish mollusc *Mytilopsis ornithopsis* Brusina, the footwall of the outcrop at Mataschen has been correlated to the *Mytilopsis ornithopsis*-zone (Pannonian, “zone” B sensu Papp 1951) (Harzhauser 2004). In the same level, *Trapa silesiaca* Göppert has been reported (Meller & Hofmann 2004). The recent monographical investigation of Trapaceae (Kovar-Eder & Wójcicki 2005) showed that in Europe unambiguous *Trapa* morphotypes are available only from the late Miocene onwards. Moreover, the presence and abundance of *Platanus leucophylla* and of *Buxus pliocenica*

indicate at least a late middle Miocene to late Miocene age. These biological correlations are also supported by the regional geological situation: an older age of the Feldbach Formation is unlikely.

The plant assemblage from the hanging wall of the Mataschen outcrop yields several taxa that are well known from older sediments of Central Europe and which have now been documented for the first time from the late Miocene of Central Europe: cf. *Distylium heinickei*, *Laurophyllum pseudovillense*, *Laurus abchasica*, *Magnolia liblarensis*, *Nyssa* cf. *haidingeri*, *Symplocos rara*, *Trigonobalanopsis rhamnoides*, cf. *Dicotylophyllum dieteri*. For cf. *Distylium heinickei*, *Laurophyllum pseudovillense*, *Nyssa* cf. *haidingeri*, *Symplocos rara*, and cf. *Dicotylophyllum dieteri*, the records from Mataschen are the youngest available. *Laurus abchasica*, *Magnolia liblarensis*, and *Trigonobalanopsis rhamnoides*, wide-spread in the early and early middle Miocene, still thrived during the late Miocene/early Pliocene in climatically favourable regions of southern Europe and the Lower Rhine Basin. If presence and abundance of *Daphnogene polymorpha*, cf. *Distylium heinickei*, *Laurophyllum pseudovillense*, *Laurus abchasica*, *Magnolia liblarensis*, *Nyssa* cf. *haidingeri*, *Symplocos rara*, *Trigonobalanopsis rhamnoides*, and cf. *Dicotylophyllum dieteri* would be taken into account exclusively, an older age of the flora from Mataschen, probably early middle Miocene, would appear more likely.

## CONCLUSIONS

The early Pannonian (late Miocene) flora from the upper part of the sedimentary sequence of Mataschen, eastern Styria (Eastern Styrian Basin, Austria), has been investigated. More than 550 mostly fragmentarily but organically preserved specimens were collected. Of these, more than 400 have been assigned to 38 taxa mostly based on cuticular analysis. The only reported conifer is *Glyptostrobus europaeus*. Deciduous taxa are not diverse and include *Acer tricuspidatum*, *Alnus menzelii*, cf. *Betula*, *Fagus*, *Platanus leucophylla*, and *Ulmus carpinooides*. The diversity of azonal taxa is low; among them, only *Myrica lignitum*, *Platanus leucophylla*, and *Ulmus carpinooides* are abundant, whereas *Glyptostrobus europaeus*, *Alnus*,

*Acer tricuspidatum*, and *Nyssa* cf. *haidingeri* occur in single or few specimens only. 27 taxa (more than two-thirds) may be regarded as being zonal, and 60% of these were most likely evergreen. Among these, *Dicotylophyllum uhlderi* Kovar-Eder sp. n. (Ericaceae), *Gordonia emanuelii* Kovar-Eder sp. n., *G. pannonica* Kovar-Eder sp. n., *G. styriaca* Kovar-Eder sp. n., *Schima mataschensis* Kovar-Eder sp. n., and "Quercus" *rhenanasimilis* Kovar-Eder sp. n. are described for the first time. *Symplocos rara* Kovar-Eder sp. n. is introduced.

Based on their occurrence in Mataschen, the stratigraphic range of cf. *Dicotylophyllum dieteri*, *Distylium* (cf. *Distylium heinickei*), *Laurophyllum pseudovillense*, *Laurus abchasica*, *Magnolia liblarensis*, *Nyssa* cf. *haidingeri*, *Symplocos rara*, and *Trigonobalanopsis rhamnoides* is extended in Central Europe into the late Miocene.

Based on the leaf fragments found in Mataschen, the geographical range of *Oleinites liguricus* probably is extended from northern Italy (Messinian) to the Paratethys region, and *Smilax* cf. *protolanceaefolia* is reported from Austria for the first time.

The high diversity of evergreen taxa and the species composition indicate close relations of the Mataschen flora to floras of the early/early middle Miocene of the Younger Mastixioid type. The mixture of evergreen taxa (partly characteristic for early/early middle Miocene floras of Central Europe, partly so far unknown from the rich European record, i.e. the newly described Ericaceae, Fagaceae, and Theaceae) and deciduous taxa (e.g. *Fagus*, *Platanus leucophylla*) along with *Oleinites* cf. *liguricus* further indicates relations to late Miocene/Pliocene floras in southern parts of Europe (Romania, Northern Italy, Greece). In comparison, the similarities to the rich late Miocene middle European plant record are rather poor.

Based on the semiquantitative evaluation, the "zonal subtropical evergreen broad-leaved forest" is the most suitable zonal vegetation unit for the flora of Mataschen. This is consistent with the purely sociological evaluation, which indicates the closest modern forest analogs to be the evergreen sclerophyllous broad-leaved forests (sensu Wang 1961) or, in other terms, the evergreen oak-laurel forests in southern parts of China, Burma, Vietnam, in southern parts of Japan and on

Taiwan. There, the main climate parameters are a MAT of about 15–19°C, MAP 1280–1950 mm, no month with an average temperature below 0°C, and occasional frosts. Due to the presence of deciduous taxa (e.g. cf. *Betula*, *Fagus*) characteristic of the ecotone towards mixed mesophytic forests today, lower to middle values of this temperature regime are more probable for the Mataschen flora. For the precipitation regime, middle to higher values are more reasonable.

The here described flora differs from the so far available, rich late Miocene floristic record in this part of Europe. This raises the question whether the flora reflects a local, climatically favourable refuge or/and a favourable climate fluctuation. No definitive answer can be given yet. Our results clearly underline the necessity of continuing investigations on new fossil plant sites and of not shunning enormously time-consuming cuticular studies to evaluate floras of a poor macro-morphological preservation state.

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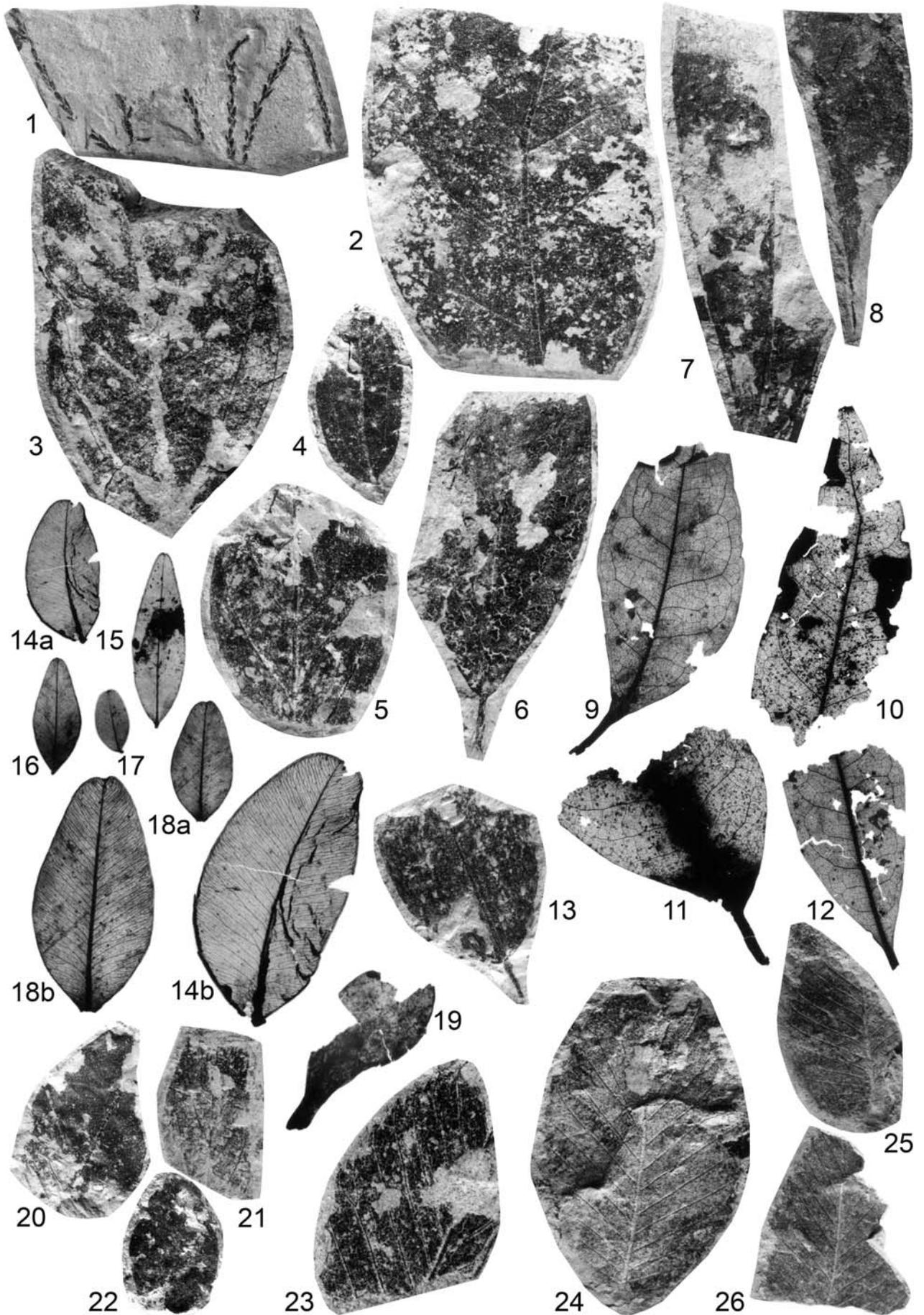
# PLATES

If not indicated differently, all specimens from the collection NHMW

Plate 1

If not indicated differently, all pictures 1×

1. *Glyptostrobus europaeus* (Brongniart) Unger coll. file no. 2000B0015/208
2. *Laurus abchasicus* (Kolakovsky & Shakryl) Ferguson, coll. file no. 2000B0015/27
- 3–6. *Daphnogene polymorpha* (Al. Braun) Ettingshausen, 3 – coll. file no. 2000B0015/361, 4 – coll. file no. 2000B0015/78, 5 – coll. file no. 2000B0015/230, 6 – coll. file no. 2000B0015/319 A
- 7–8. *Magnolia liblarensis* (Kräusel & Weyland) Kvaček, 7 – coll. file no. 2000B0015/55, 8 – coll. file no. 2000B0015/321 A
- 9–12. *Laurophyllum pseudoprinceps* Weyland & Kilpper, 9 – coll. file no. 2000B0015/581, 10 – coll. file no. 2000B0015/525, 11 – coll. file no. 2000B0015/526, 12 – coll. file no. 2000B0015/584
13. *Laurophyllum* sp., coll. file no. 2000B0015/6
- 14–18. *Buxus pliocenica* Saporta & Marion, 14 a, b – coll. file no. 2000B0015/538, b – 2×, 15 – coll. file no. 2000B0015/547, 16 – coll. file no. 2000B0015/550, 17 – coll. file no. 2000B0015/535, 18 a, b – coll. file no. 2000B0015/599, b – 2×
19. *Viscum morlotii* (Unger) Knobloch & Kvaček, coll. file no. 1998B0014/630
20. cf. *Distylium heinickei* Walther, coll. file no. 2000B0015/72 A
21. ? *Corylopsis* sp., coll. file no. 2000B0015/9
22. *Rosa* sp., coll. file no. 2000B0015/210
- 23–26. *Ulmus carpinoides* Göppert sensu Menzel, 23 – coll. file no. 2000B0015/106, 1.5×, 24 – coll. file no. 2000B0015/117, 25 – coll. file no. 2000B0015/123, 26 – coll. file no. 2000B0015/326



## Plate 2

If not indicated differently, all pictures 1 ×

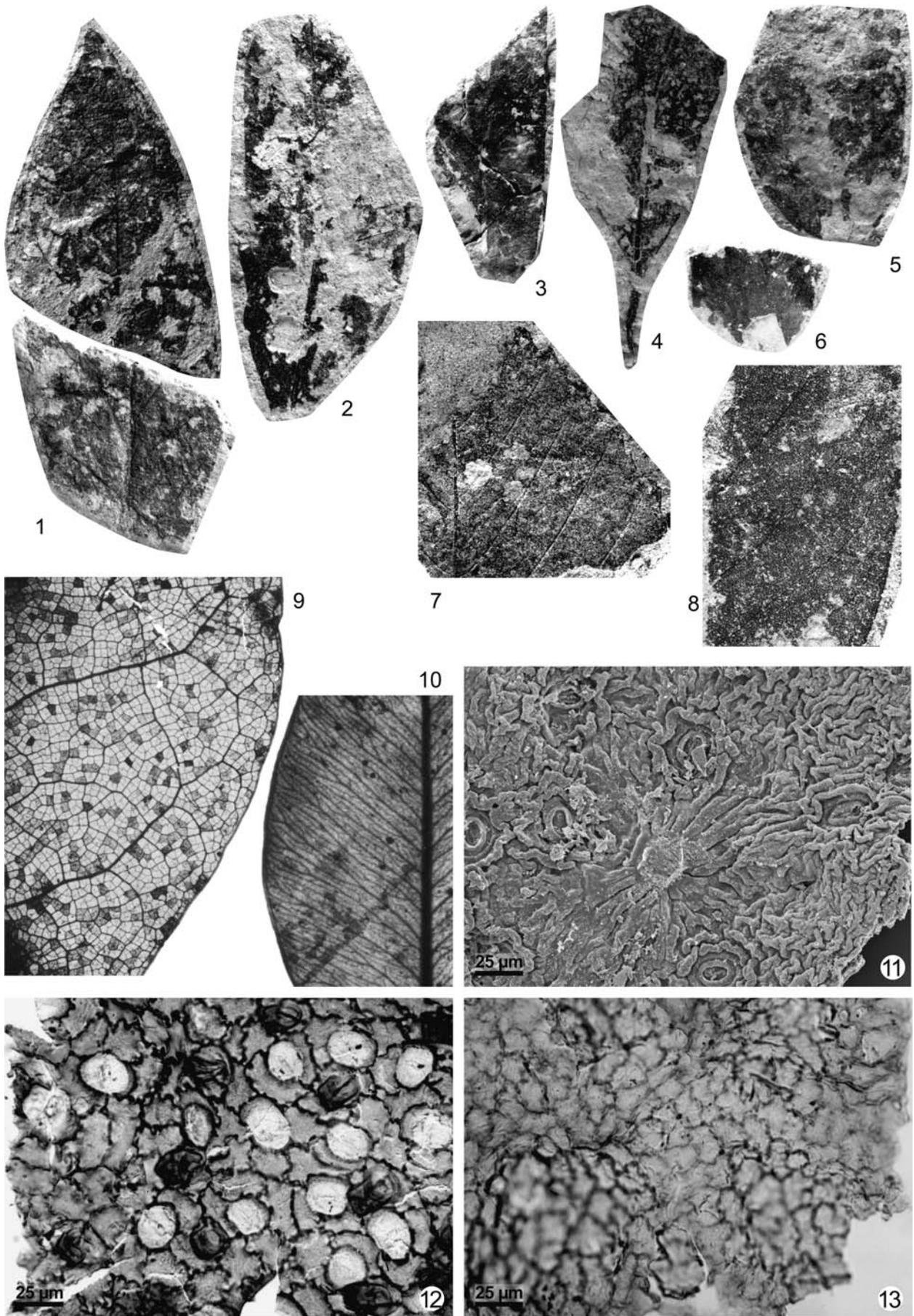
- 1–4. *Platanus leucophylla* (Unger) Knobloch, 1 – coll. file no. 2000B0015/456, 2 – coll. file no. 2000B0015/322 A, 3 – coll. file no. 2000B0015/117 A, 4 – coll. file no. 2000B0015/32
- 5–6. *Fagus* sp., 5 – coll. file no. 2000B0015/112, 6 – coll. file no. 2000B0015/244
7. ? *Fagus* vel *Sloanea* sp., coll. file no. 2000B0015/342
8. “*Quercus*” *rhenanasimilis* Kovar-Eder sp. n., holotype, coll. file no. 2000B0015/207
- 9–10. cf. *Betula* sp., 9 – coll. file no. 2000B0015/403, 10 – coll. file no. 2000B0015/306
- 11–13. *Alnus menzelii* Raniecka-Bobrowska, 11 – coll. file no. 2000B0015/120, 12 – coll. file no. 2000B0015/304 C, 13 – coll. file no. 2000B0015/304 B
14. *Alnus* sp., coll. file no. 2000B0015/53 A
- 15–17. *Myrica lignitum* (Unger) Saporta, 15 – coll. file no. 2000B0015/452, 16 – coll. file no. 2000B0015/305, 17 – coll. file no. 2000B0015/125
18. *Symplocos rara* Kovar-Eder sp. n., holotype, coll. file no. 2000B0015/115
- 19–20. *Gordonia emanuelii* Kovar-Eder sp. n., 19 – paratype, coll. file no. 2000B0015/28, 20 – paratype, coll. file no. 2000B0015/333
- 21–23. *Gordonia pannonica* Kovar-Eder sp. n., 21 – paratype, coll. file no. 2000B0015/7, 22 – paratype, coll. file no. 2000B0015/259, 23 – paratype, coll. file no. 2000B0015/206



## Plate 3

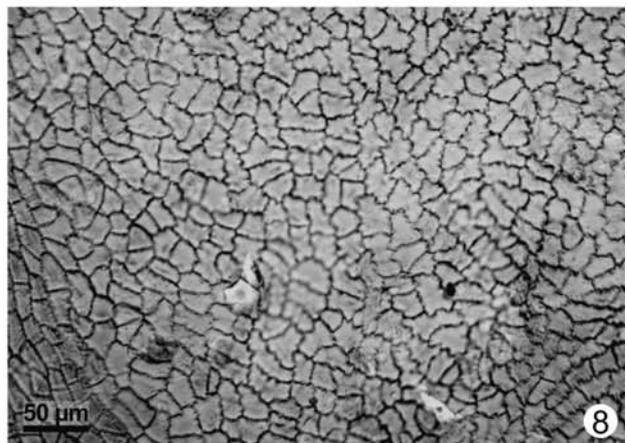
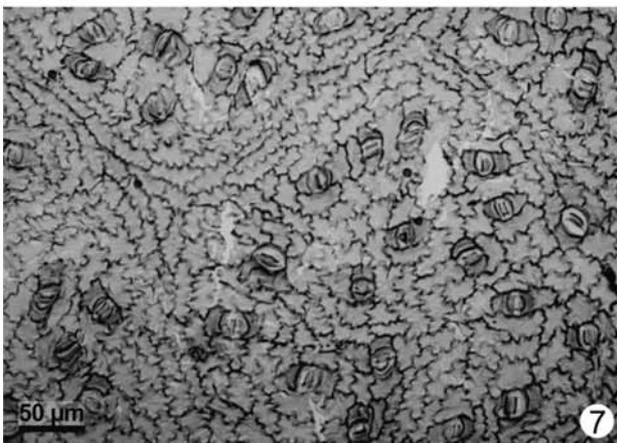
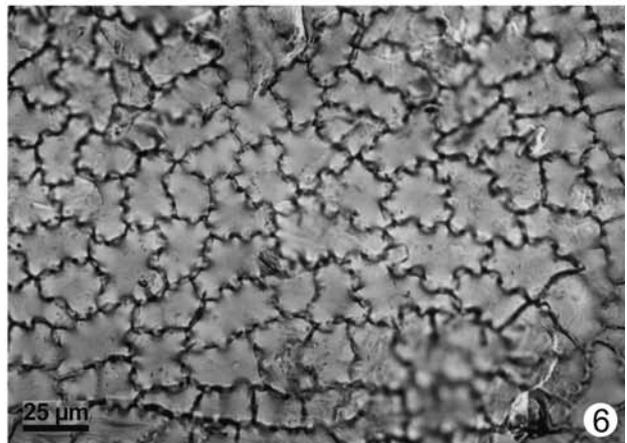
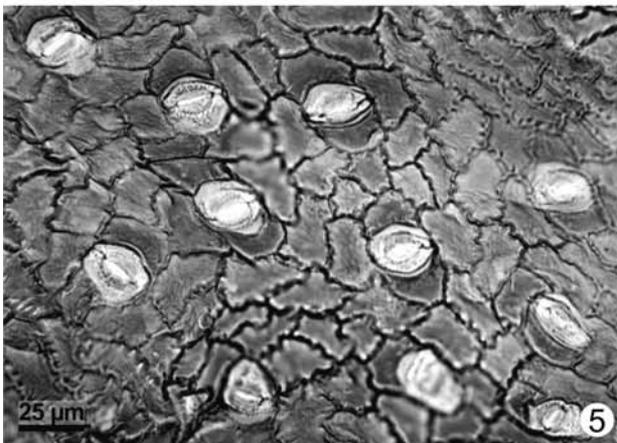
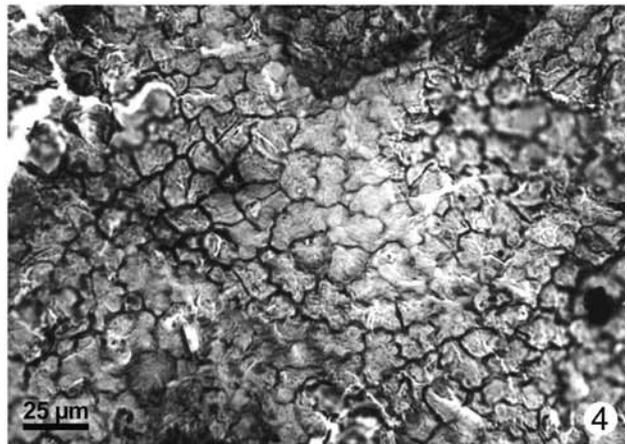
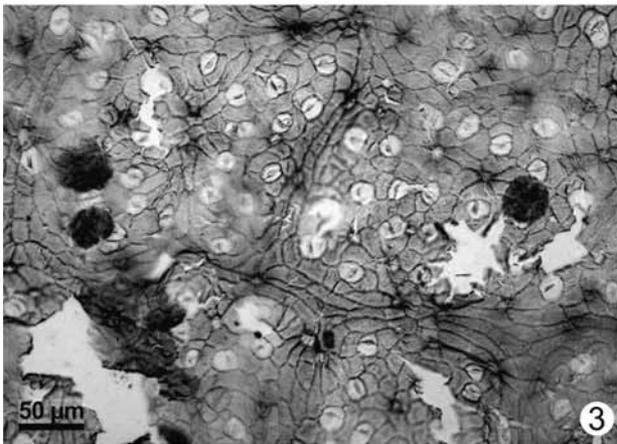
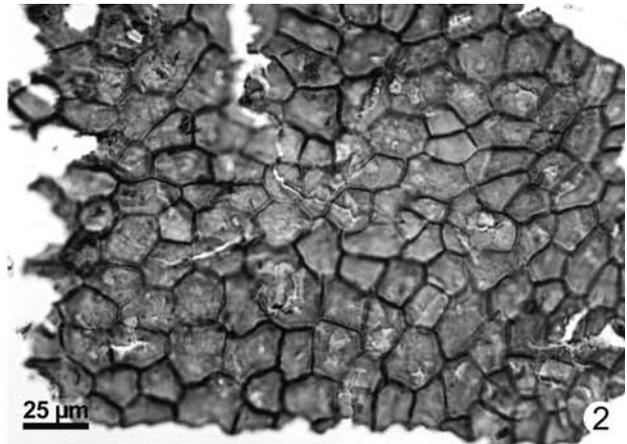
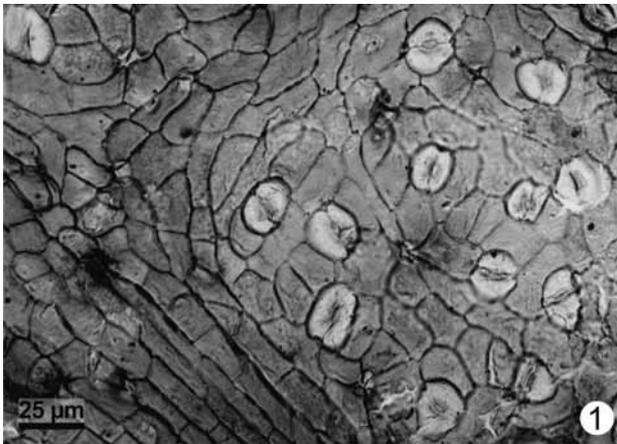
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- 1–3. *Dicotylophyllum uhudler* Kovar-Eder sp. n., 1 – upper part, paratype, coll. file no. 2000B0015/301, lower part, paratype coll. file no. 2000B0015/150, 2 – paratype, coll. file no. 2000B0015/114, 3 – paratype, coll. file no. 2000B0015/441
4. *Schima mataschensis* Kovar-Eder sp. n., holotype, coll. file no. 2000B0015/222 B
5. *Smilax* cf. *protolanceaefolia*, coll. file no. 2000B0015/347
6. *Oleinites* cf. *liguricus* Sachse, coll. file no. 2000B0015/426
7. cf. *Betula* sp., double serrate leaf margin, coll. file no. 2000B0015/306, 1.5 ×
8. *Magnolia liblarensis* (Kräusel & Weyland) Kvaček, venation pattern, coll. file no. 2000B0015/321 A, 2 ×
9. *Laurophyllum pseudoprinceps* Weyland & Kilpper, details of venation pattern, coll. file no. 2000B0015/526, 4 ×
10. *Buxus pliocenica* Saporta & Marion, details of venation pattern, coll. file no. 2000B0015/599
11. *Dicotylophyllum uhudler* Kovar-Eder sp. n., abaxial cuticle, SEM, outer surface strongly wrinkled, stomata and trichome/gland remain, paratype, coll. file no. 2000B0015/1
- 12, 13. *Magnolia liblarensis* (Kräusel & Weyland) Kvaček, 12 – abaxial cuticle with brachyparacytic stomatal complexes, trichome bases with adherent remains of the trichome foot, coll. file no. 2000B0015/233/2; 13 – adaxial cuticle, coll. file no. 2000B0015/233/1



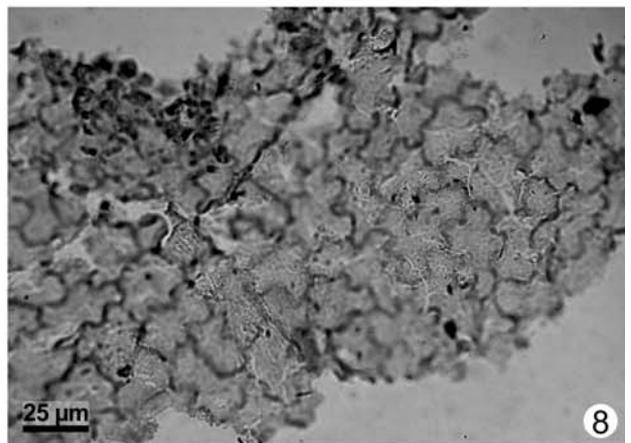
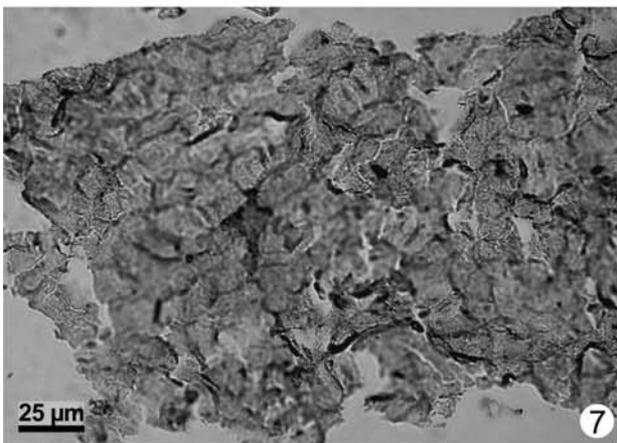
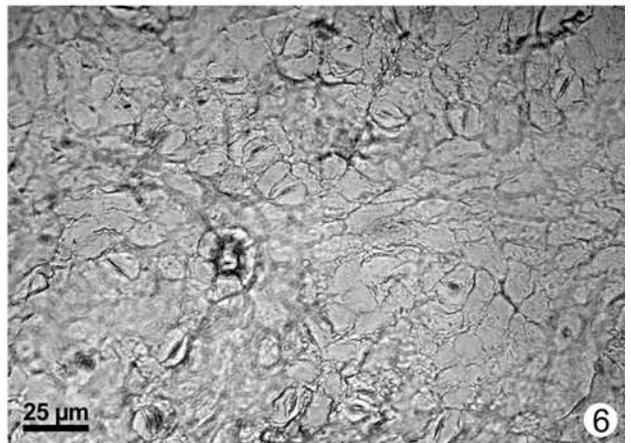
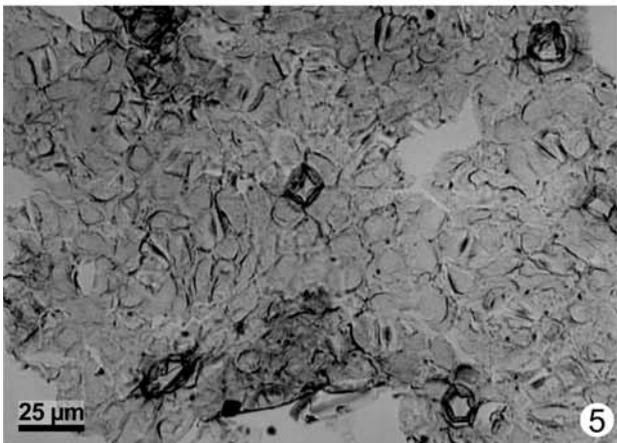
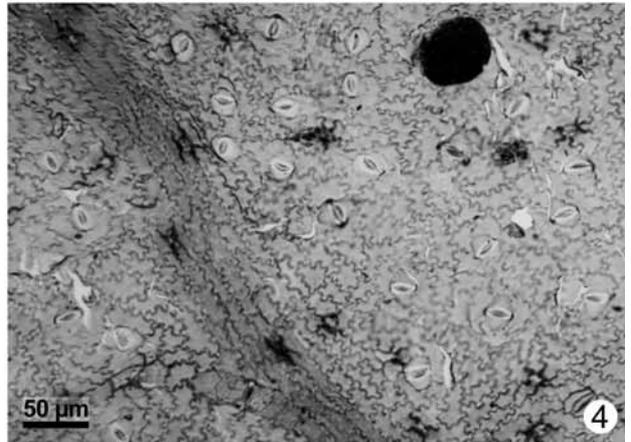
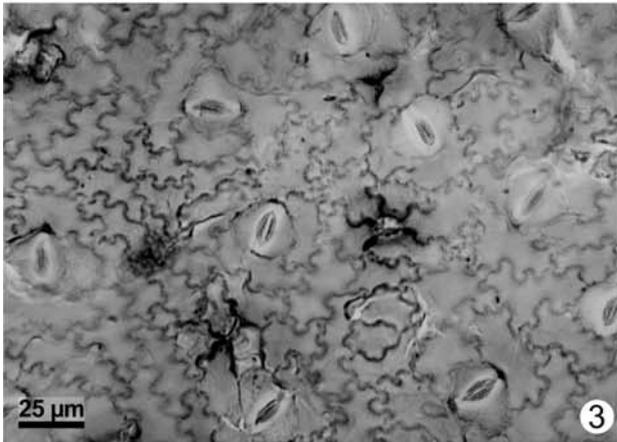
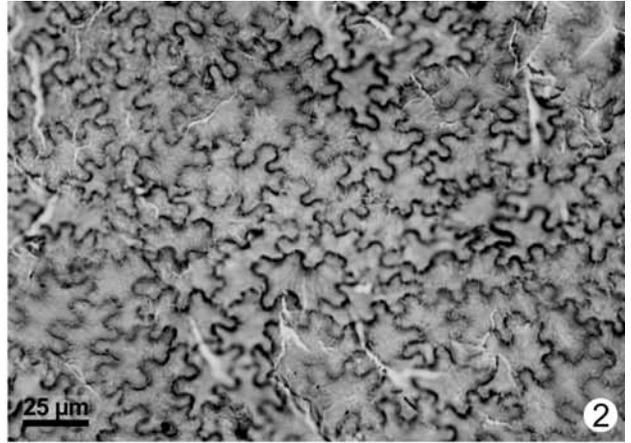
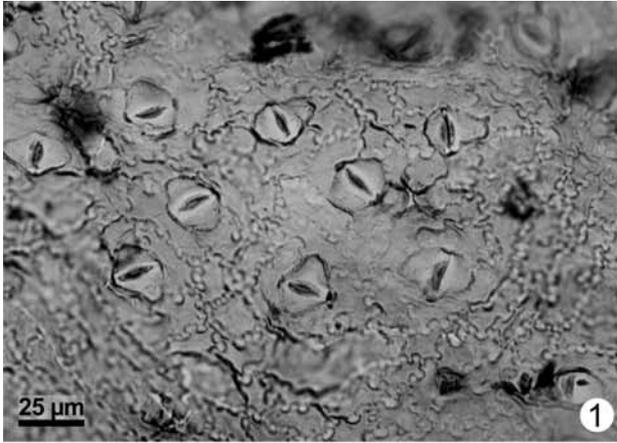
## Plate 4

- 1–4. *Daphnogene polymorpha* (Al. Braun) Ettingshausen, 1 – abaxial cuticle, 2 – adaxial cuticle, anticlines almost straight, 1 and 2 – coll. file no. 2000B0015/26 B/1, 3 – abaxial cuticle and secretory bodies, coll. file no. 2000B0015/113 A, 4 – adaxial cuticle, anticlines wavy to undulate, coll. file no. 2000B0015/191/1
- 5–8. *Laurophyllum pseudoprinceps* Weyland & Kilpper, 5, 7 – abaxial cuticle, 6, 8 – adaxial cuticle, 5, 6, 8 – coll. file no. 2000B0015/539, 7 – coll. file no. 2000B0015/139



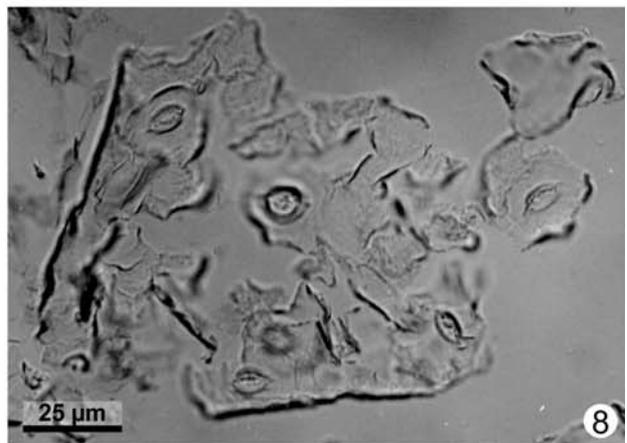
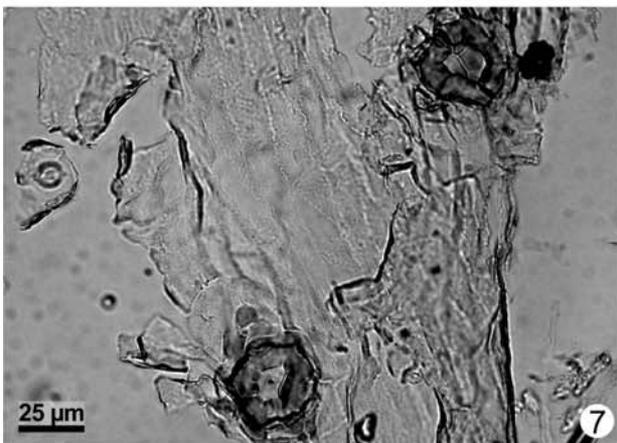
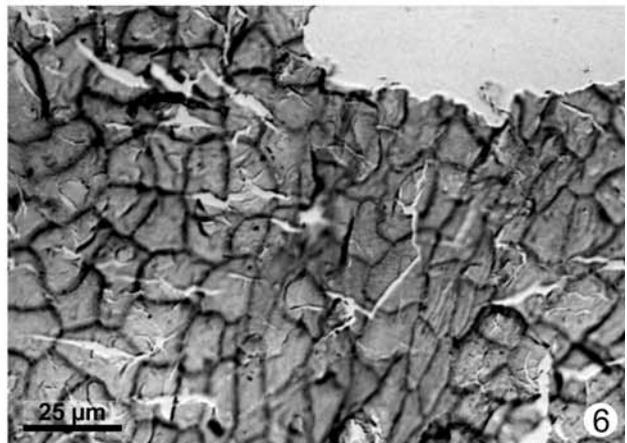
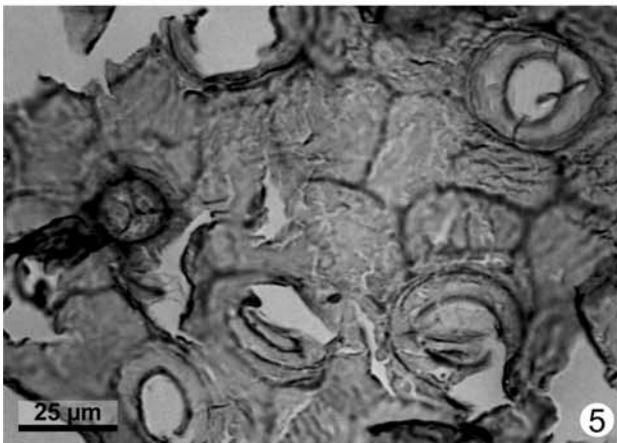
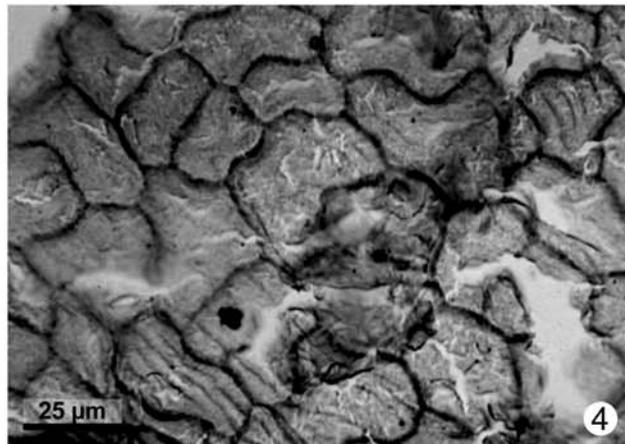
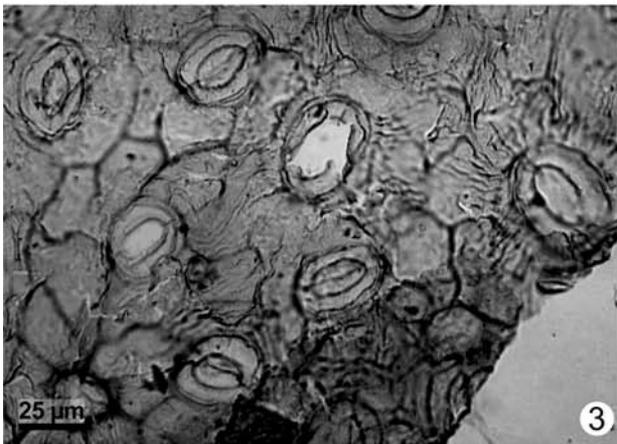
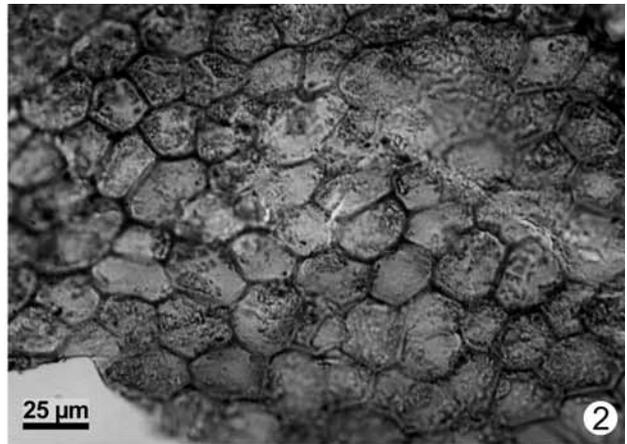
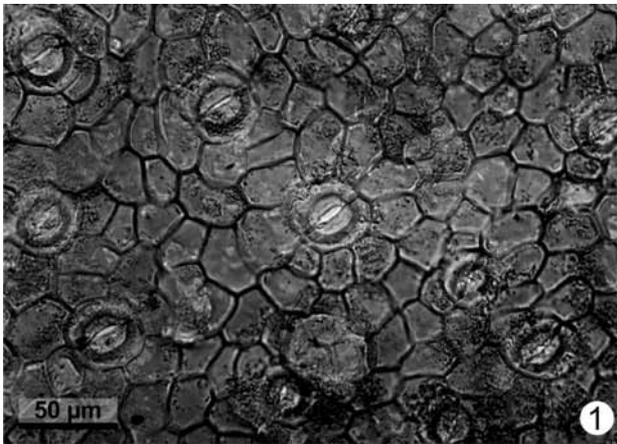
## Plate 5

- 1–4. *Laurus abchasica* (Kolakovsky & Shakryl) Ferguson, 1, 3, 4 – abaxial cuticle, simple trichome bases scattered, secretory body, 2 – adaxial cuticle, 1 – coll. file no. 2000B0015/23, 2–4 – coll. file no. 2000B0015/461 B
- 5, 6. *Laurophyllum pseudovillense* Kvaček, 5 – abaxial cuticle, non-modified epidermal cells slightly dome-shaped, several characteristic trichome bases coll. file no. 2000B0015/360, 6 – holotype refigured for comparison, coll. PRC, no. KR-265, Hradek n. N., Bohemia, orig. Kvaček & Bůžek 1966, pl. 1 fig. 6, pl. 2 fig. 1; Kvaček 1971, pl. 11 figs 1–3
- 7, 8. *Laurophyllum* sp., 7 – abaxial cuticle, 8 – adaxial cuticle, 7, 8 – coll. file no. 2000B0015/6



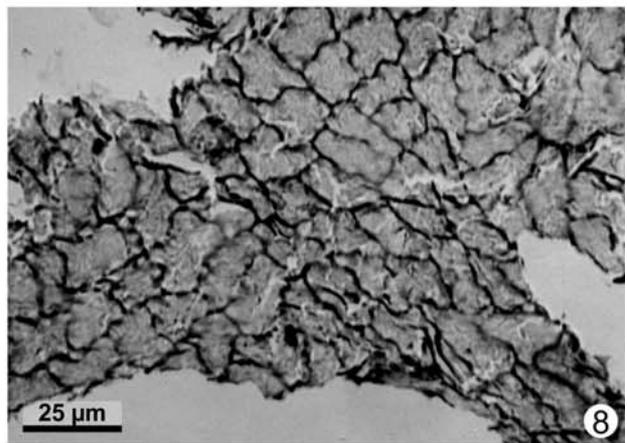
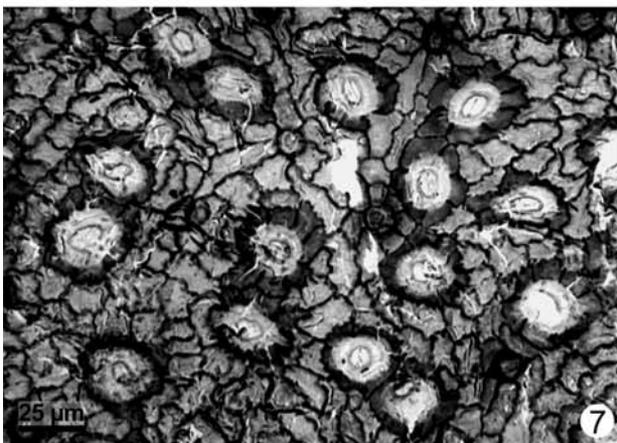
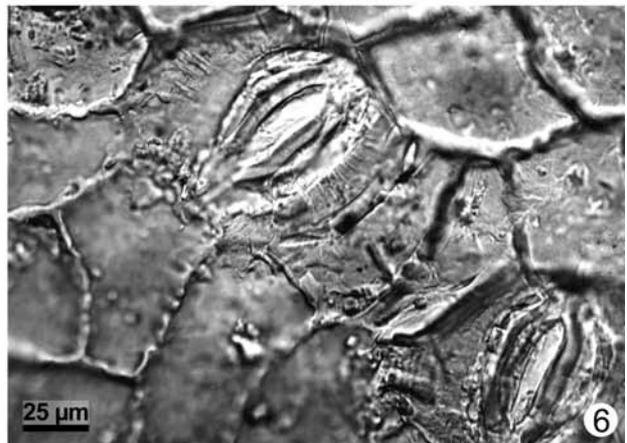
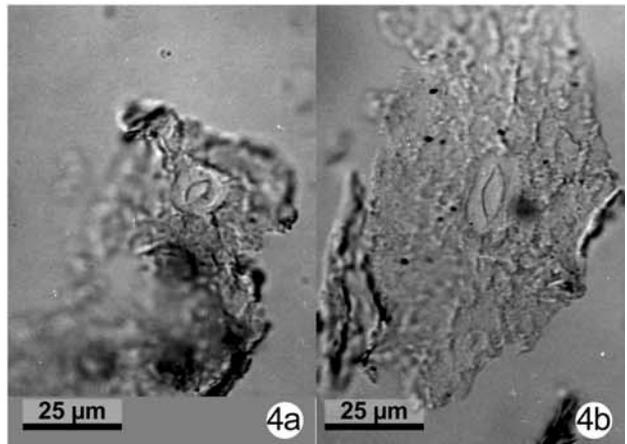
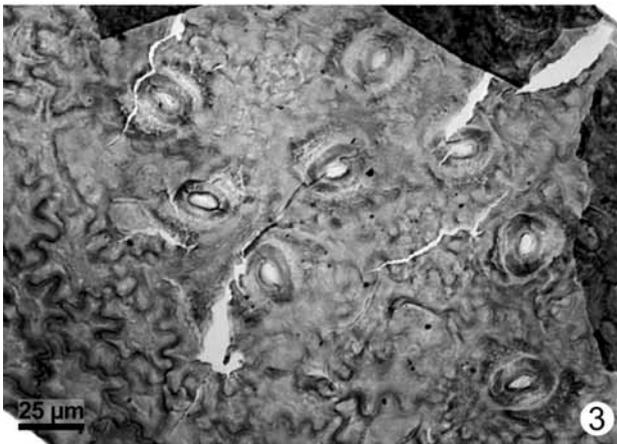
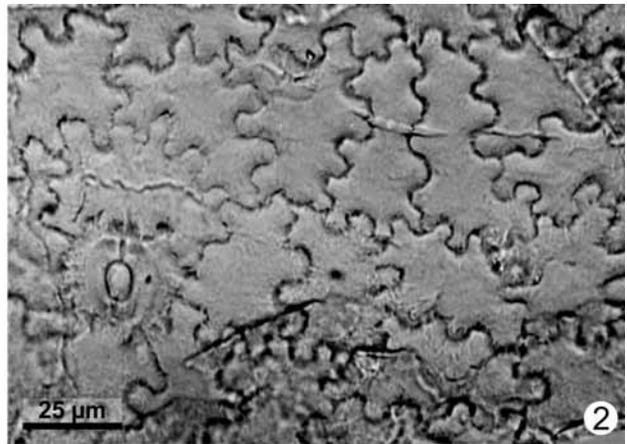
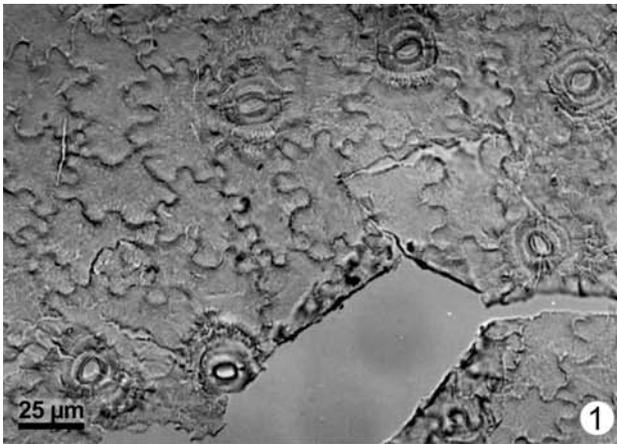
## Plate 6

- 1, 2. *Buxus pliocenica* Saporta & Marion, 1 – abaxial cuticle, 2 – adaxial cuticle, 1 – coll. file no. 2000B0015/16 A/2, 2 – coll. file no. 2000B0015/16 A/1
- 3–6. *Platanus leucophylla* (Unger) Knobloch, 3, 5 – abaxial cuticle with cyclocytic stomata and distinct striation and with a pluricellular trichome base and adherent trichome fragment in picture 5; 4, 6 – adaxial cuticle, 3, 6 – coll. file no. 2000B0015/32/3, 4, 5 – coll. file no. 2000B0015/54
- 7, 8. ? *Corylopsis* sp., 7 – abaxial cuticle with prominent trichome bases on a vein and a single stoma, 8 – abaxial cuticle, 7, 8 – coll. file no. 2000B0015/91



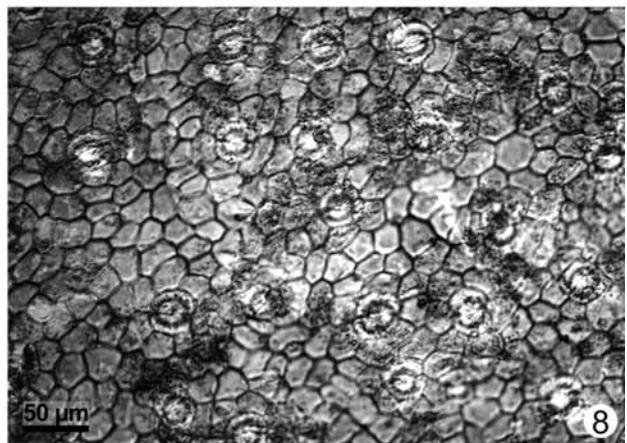
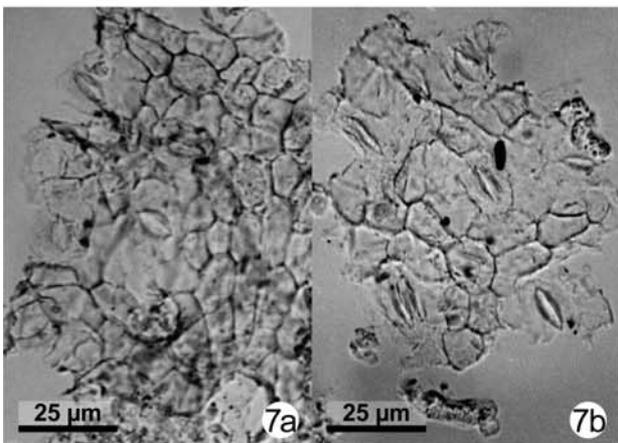
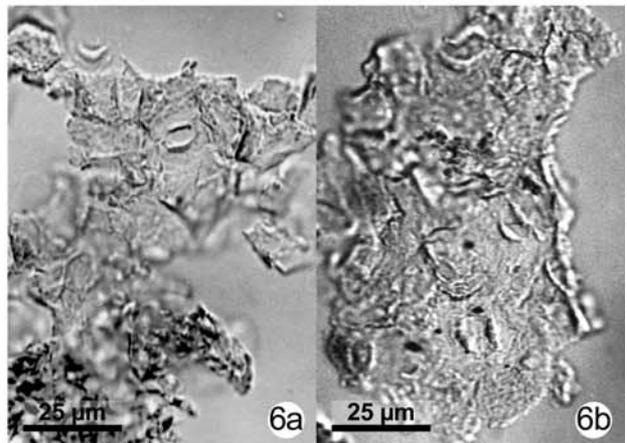
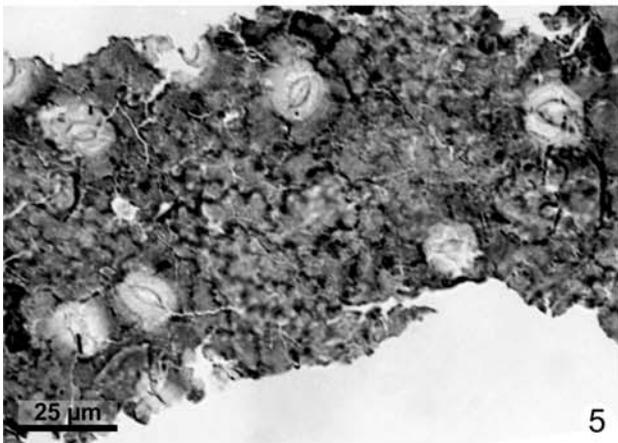
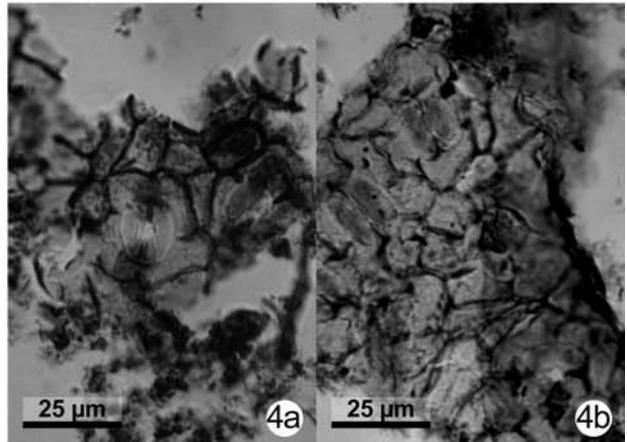
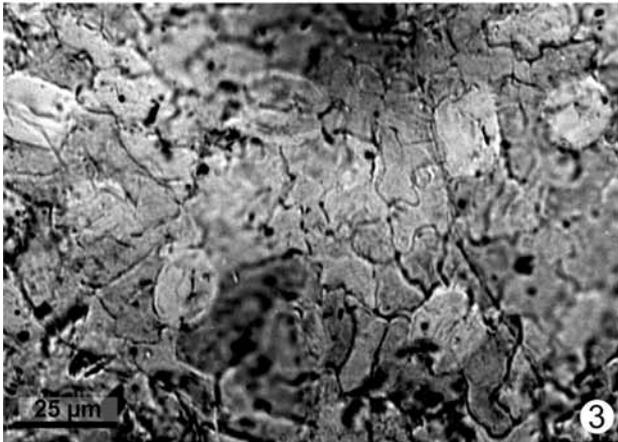
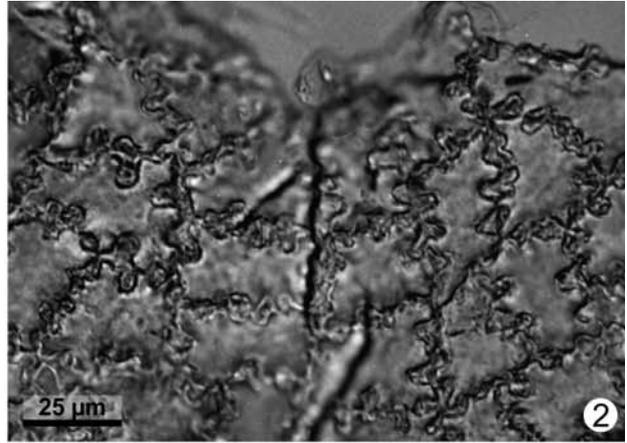
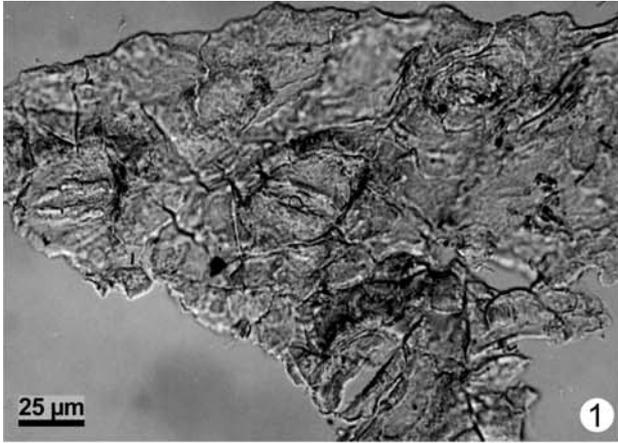
## Plate 7

- 1–3. cf. *Distylium heinickei* Walther, 1, 3 abaxial cuticle, glabrous, 2 – abaxial and adaxial cuticle, 1, 2 – coll. file no. 2000B0015/339 A, 3 – coll. file no. 2000B0015/72 A
- 4a,b. *Rosa* sp., tiny fragments of the abaxial cuticle, a, b – coll. file no. 2000B0015/35
- 5, 6. *Viscum morlotii* (Unger) Knobloch & Kvaček, cuticle in stomatal condition, coll. file no. 2000B0015/618
- 7, 8. *Trigonobalanopsis rhamnoides* (Rossmässler) Kvaček & Walther, 7 – abaxial cuticle with densely spaced cyclocytic stomatal complexes and simple trichome bases, 8 – adaxial cuticle, coll. file no. 2000B0015/362/1



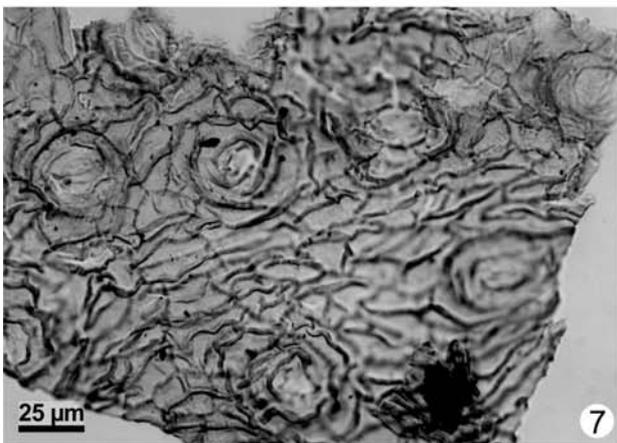
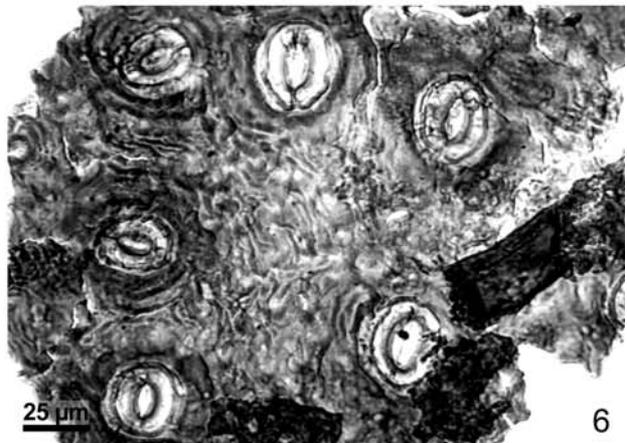
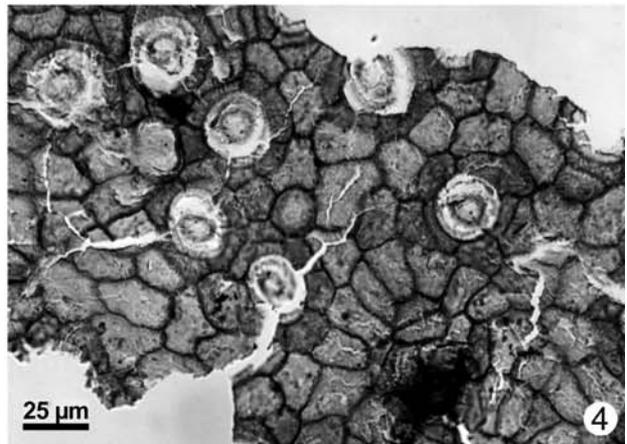
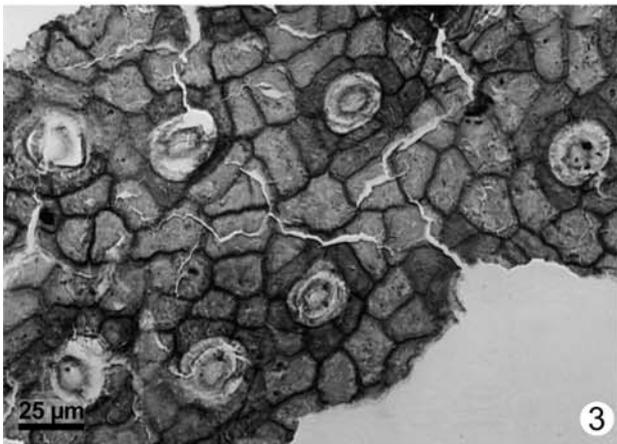
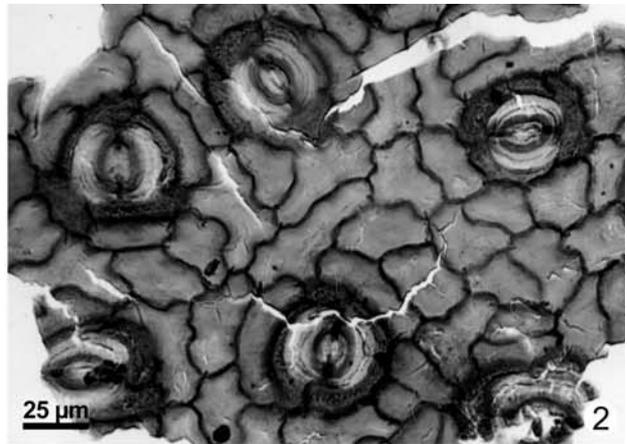
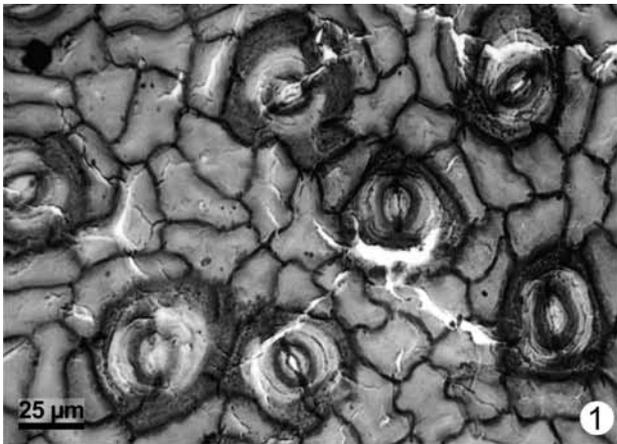
## Plate 8

- 1, 2. "*Quercus*" *rhenanasimilis* Kovar-Eder sp. n., 1 – abaxial cuticle with a single simple trichome base, 2 – adaxial cuticle with very narrowly U to  $\Omega$ -shaped undulate anticlines, 1, 2 – holotype, coll. file no. 2000B0015/207
3. *Fagus* sp., abaxial cuticle, coll. file no. 2000B0015/244
- 4a,b. *Quercus kubinyii* (Kovats ex Ettingshausen) Czegezott, abaxial cuticle, a, b – coll. file no. 2000B0015/113 B
5. ?*Fagus* vel *Sloanea* sp., abaxial cuticle, coll. file no. 2000B0015/342
- 6a,b. *Acer tricuspidatum* Bronn, abaxial cuticle, a – coll. file no. 2000B0015/48/1, b – coll. file no. 2000B0015/48/2
- 7a,b. Betulaceae gen. et sp. indet., a, b – abaxial cuticle with pluricellular trichome base in a; a, b – coll. file no. 2000B0015/108 A
8. *Buxus pliocenica* Saporta & Marion, abaxial cuticle, coll. file no. 2000B0015/16 A/1



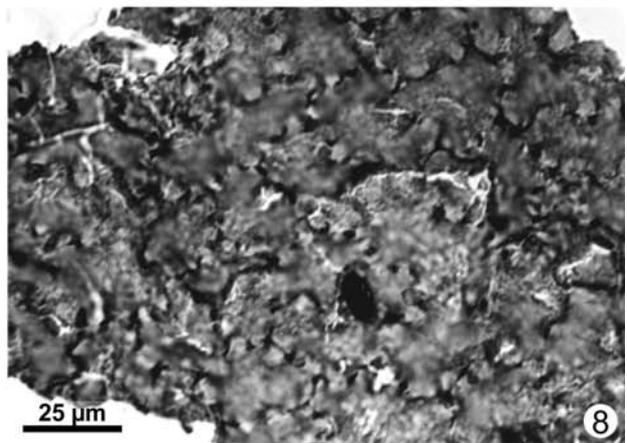
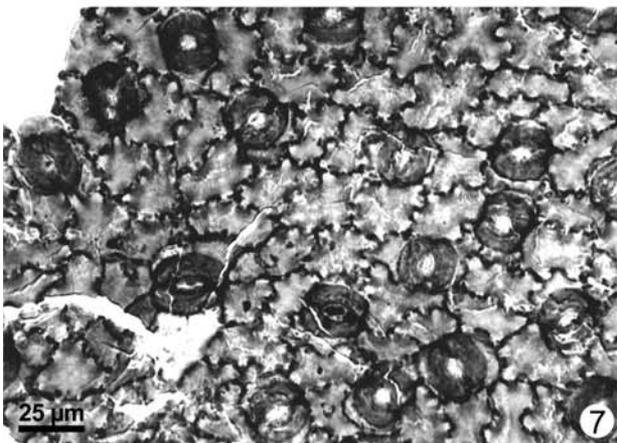
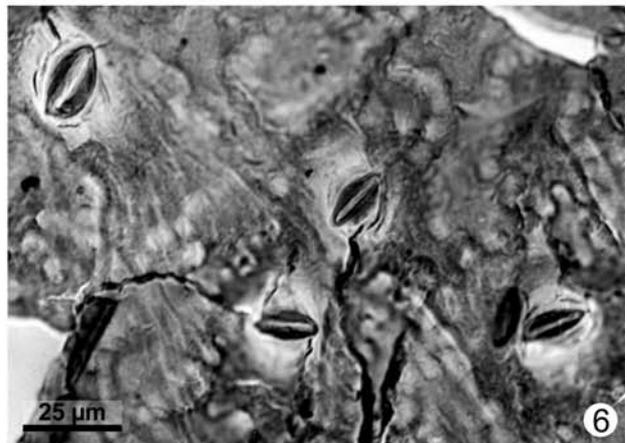
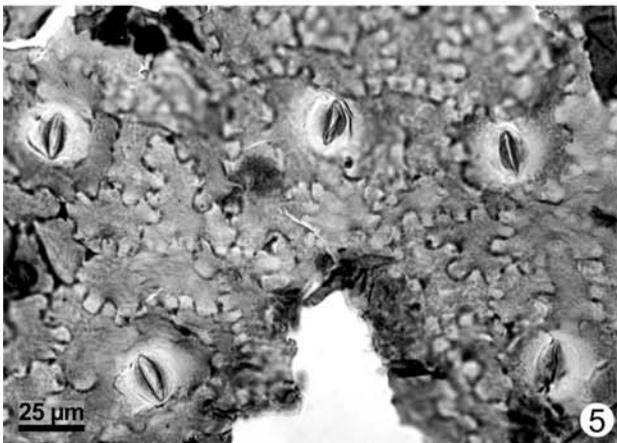
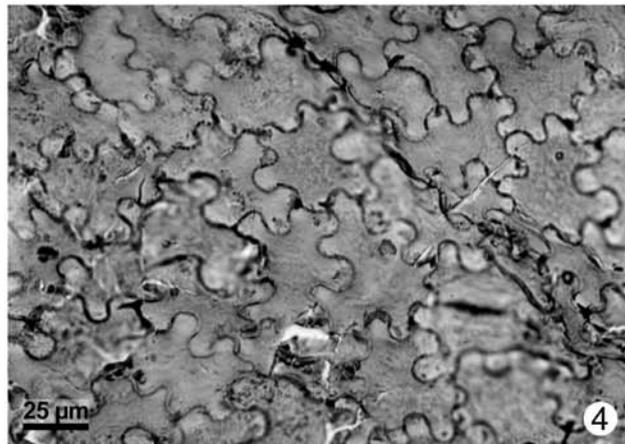
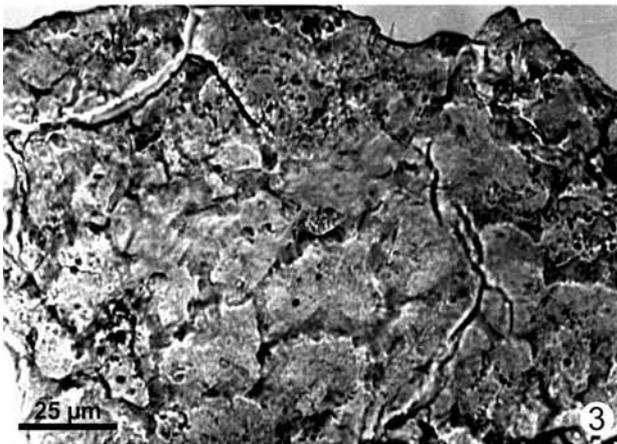
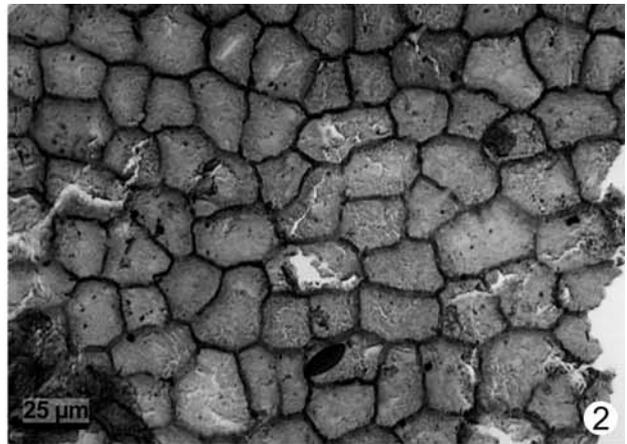
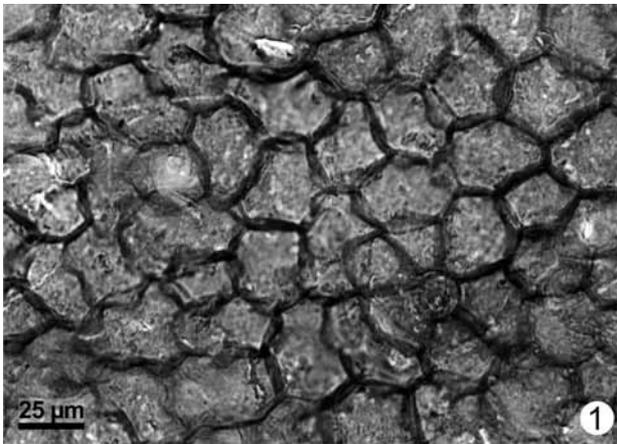
## Plate 9

- 1, 2. *Gordonia emanuelii* Kovar-Eder sp. n., abaxial cuticle, holotype, coll. file no. 2000B0015/241 A
- 3, 4. *Gordonia styriaca* Kovar-Eder sp. n., abaxial cuticle, holotype, coll. file no. 2000B0015/10 B
- 5, 6. *Gordonia pannonica* Kovar-Eder sp. n., abaxial cuticle, 5 – holotype, coll. file no. 2000B0015/149, 6 – paratype, coll. file no. 2000B0015/17
- 7, 8. *Schima mataschensis* Kovar-Eder sp. n., 7 – abaxial cuticle, 8 – cuticle upon a vein with prominent trichome bases; 7, 8 – holotype, coll. file no. 2000B0015/222 B



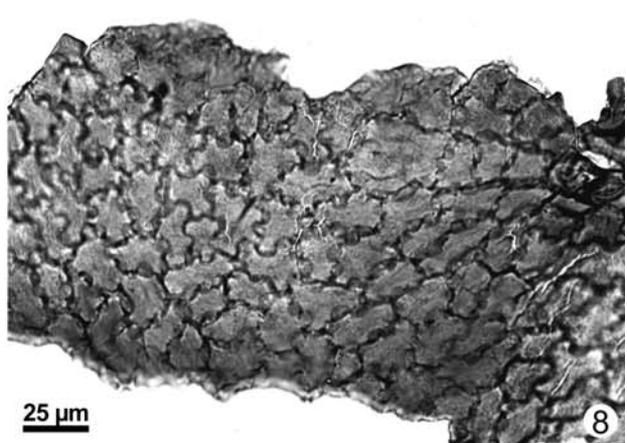
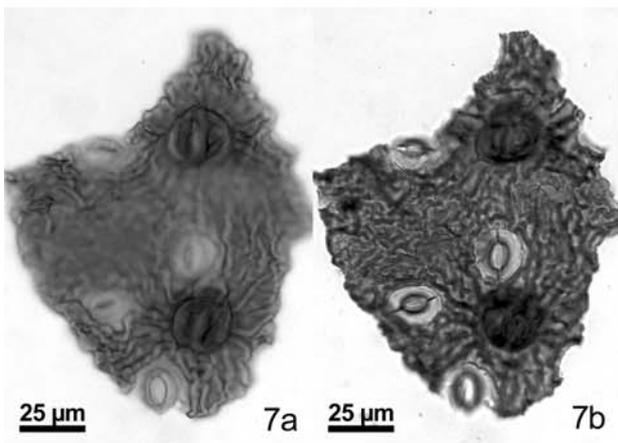
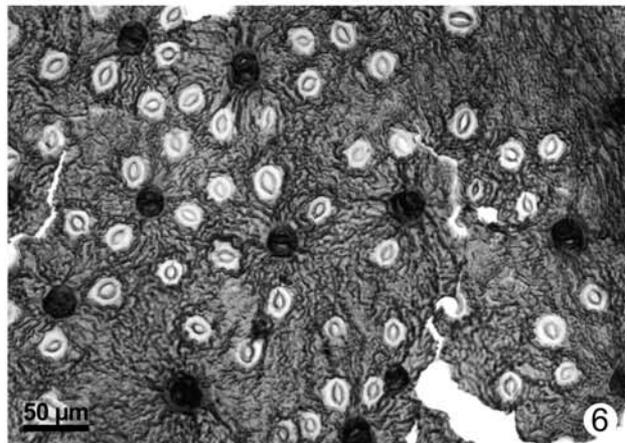
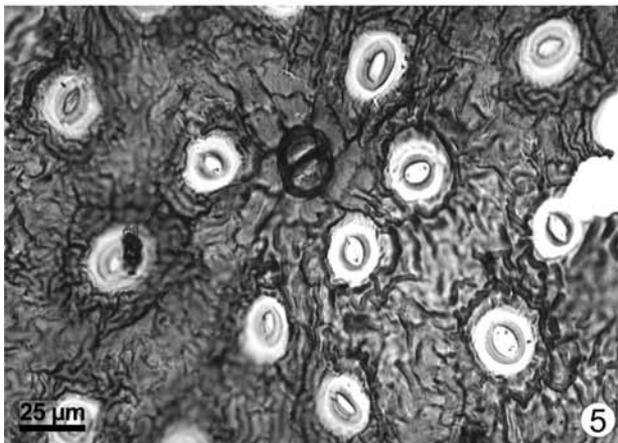
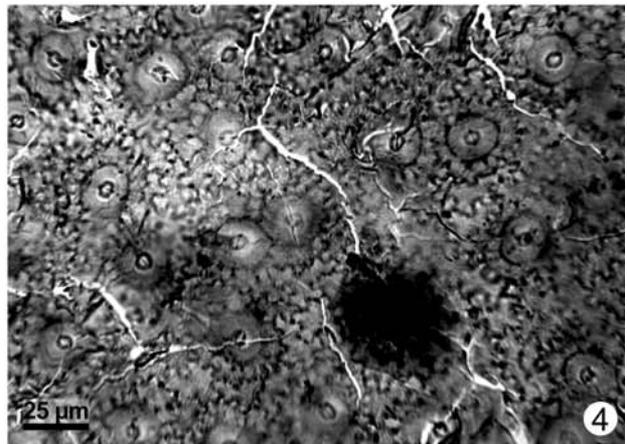
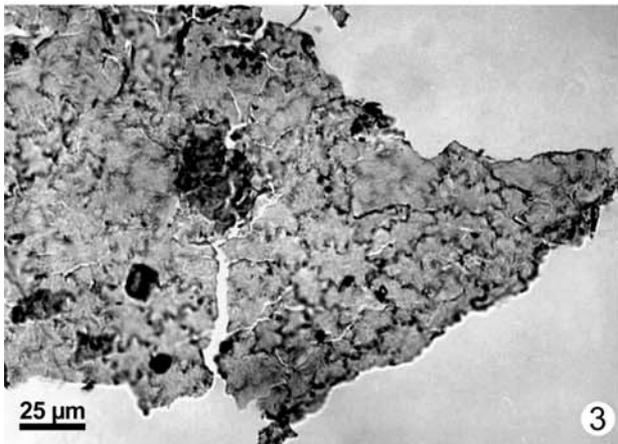
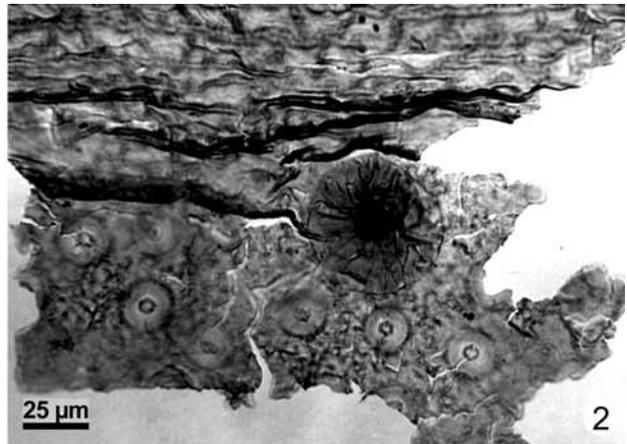
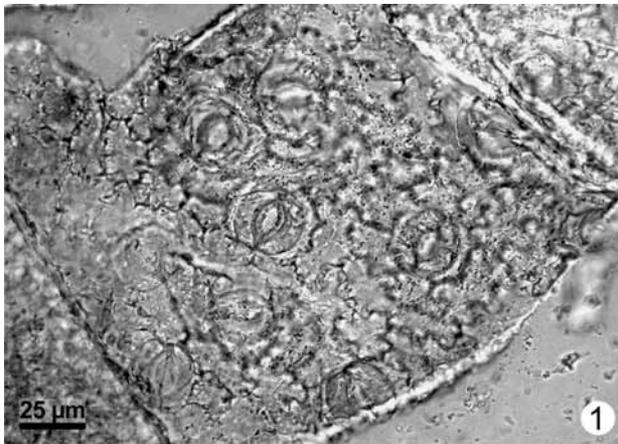
## Plate 10

1. *Gordonia emanuelii* Kovar-Eder sp. n., adaxial cuticle, paratype, coll. file no. 2000B0015/425
2. *Gordonia styriaca* Kovar-Eder sp. n., adaxial cuticle, holotype, coll. file no. 2000B0015/10 B
3. *Gordonia pannonica* Kovar-Eder sp. n., abaxial and adaxial cuticle, holotype, coll. file no. 2000B0015/149
- 4–6. *Smilax* cf. *protolanceaefolia* Kolakovsky, 4 – adaxial cuticle, 5, 6 – abaxial cuticle, 4–6 – coll. file no. 2000B0015/347
- 7, 8. *Symplocos rara* Kovar-Eder sp. n., 7 – abaxial cuticle, 8 – adaxial cuticle, 7, 8 – holotype, coll. file no. 2000B0015/115



## Plate 11

1. *Symplocos rara* Kovar-Eder sp. n. formerly *Dicotylophyllum* sp. 8, orig. Knobloch & Kvaček 1976, pl. 38, figs 8–10, coll. PRC no. Sch 439/1, abaxial cuticle
- 2–4. *Oleinites* cf. *liguricus* Sachse, 2, 4 – abaxial cuticle with peltate trichomes, 3 – adaxial cuticle, 2–4 – coll. file no. 2000B0015/426
- 5–8. *Dicotylophyllum uhudler* Kovar-Eder sp. n., 5, 6 – abaxial cuticle with characteristic pluricellular trichome bases, 7 a, b – glandular trichome, focus in two different levels, a – top of the gland, b – level of the stomata and the trichome base, 8 – adaxial cuticle, 5, 8 – paratype, coll. file no. 2000B0014/441, 6, 7 a, b – holotype, coll. file no. 2000B0015/3



## Plate 12

- 1, 2. *Myrica lignitum* (Unger) Saporta, 1 – abaxial cuticle with peltate trichomes situated above two-celled trichome bases, 2 – adaxial cuticle with peltate trichomes situated above two-celled trichome bases, 1, 2 – coll. file no. 2000B0015/432 A
- 3, 4. *Nyssa* cf. *haidingeri* (Ettingshausen) Kvaček & Bůžek, 3 – abaxial cuticle, 4 – adaxial cuticle, 3, 4 – coll. file no. 2000B0015/237
- 5, 6a,b. cf. *Dicotylophyllum dieteri* Kovar-Eder, 5 – abaxial cuticle, 6 a – cuticle fragment of non-modified epidermal cells probably from the adaxial cuticle, 6 b – a peltate trichome above an extremely thick trichome base; 5, 6 – coll. file no. 2000B0015/504 A
7. *Gordonia axillaris* (Roxb. ex Ker) Endl., China, Yunnan forest, no. 9237, N. 1912; coll. PRC; abaxial cuticle showing stomata surrounded by an inner and an almost incomplete outer circle of elongated subsidiary cells, stomata densely spaced, sometimes sharing their subsidiary cells
8. *Gordonia lasianthus* L., Nash 2089, Florida, coll. PRC, abaxial cuticle showing stomata surrounded by an inner and a mostly incomplete outer circle of partly elongated subsidiary cells, stomata densely spaced, sometimes sharing their subsidiary cells

