

# Early Oligocene plant diversity along the Upper Rhine Graben: The fossil flora of Rauenberg, Germany

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**ABSTRACT.** The macroflora of Rauenberg, Baden-Württemberg, Germany, is treated monographically. The plant-bearing sediments are marine, mainly well-bedded clay- to siltstones, the so-called Fischeschiefer, which are part of the Bodenheimer Formation. Based on nannoplankton they are dated to nannoplankton zone NP 23 (Rupelian, Lower Oligocene). The plant remains, mainly leaves and some fructifications, are preserved as compressions. The taxonomic assignment is based on gross morphology and cuticle characteristics. The flora yields marine algae and remains of the very diverse terrestrial flora. A total of 68 taxa, including three types of algae, one cycad, 12 conifers, and 49 dicots, among them 5 palms, are described. The following fossil species are described for the first time: *Laurophyllum rauenbergense*, *Myrica obliquifolia*, *Distylium metzleri*, *Berchemia altorhenana*, *Ternstroemites maritiae*, *Trachelospermum kelleri*, *Oleinites altorhenana*, *O. rauenbergensis*, *Dicotylophyllum badense*, *D. oechsleri*, *D. vesiculaeferens*, *D. ziegleri*, *Viscophyllum hendriksiae*, and *Cladites vesiculaeferens*. *Dicotylophyllum vesiculaeferens* and *Cladites vesiculaeferens* bear peculiar, complex cuticular structures presumably representing salt-secreting glands. Both taxa are interpreted to derive from one plant species of yet uncertain systematic affinity. The flora bears a high proportion of broad-leaved, presumably evergreen taxa, whereas the diversity of modern Arcto-Tertiary taxa (sensu Kvaček 1994) is rather low. Most abundant are *Platanus neptuni*, *Daphnogene cinnamomifolia*, and *Tetraclinis salicornioides*. On the family level, Lauraceae (10 species) and Pinaceae (8) are most diverse, followed by Arecaceae (4–5), Cupressaceae, and Myricaceae (4 species each). Surprisingly, Fagaceae are documented solely by a single leaf of *Eotrigonobalanus furcinervis* f. *haselbachensis*, and the record of Pentaphyllaceae remains ambiguous (*Ternstroemites maritiae*). *Sloanea olmediaefolia* is recorded for the first time from western parts of Europe. Remarkable is the presence of the rare cycad *Ceratozamia floersheimensis*. The following possible vegetation units are suggested: zonal broad-leaved sclerophyllous evergreen forests and an intrazonal coastal pine-laurel-palm association on near-coastal sandy soils, as well as gallery forests along streams. No records of swampy environments were recovered. The climate may be characterised as follows: Cfa climate in transition to Cwa (and Am or Af) climate sensu Köppen, mean annual temperature 19–24°C, mean annual precipitation 1300–1700 mm, mean temperature of the warmest month 28–29°C, mean temperature of the coldest month 8–14°C, mean precipitation of the wettest month >230 mm, mean precipitation of the driest month 18–38 mm, wettest month between May and October, driest month between November and March. The warm period was the wetter one.

The flora from Rauenberg most closely resembles that of Flörsheim (Kvaček 2004a) and shows relations to the Paratethys realm, for example the Tard Clay Formation. Relations to the floras from Saxony, Saxony-Anhalt, and North Bohemia, similar in age, are rather restricted: broad-leaved deciduous taxa are much less diverse, and the numerous presumably evergreen taxa and palms present in Rauenberg have not been recorded in the other regions, indicating a more complex vegetation differentiation than a simple north-south gradient. The high number of taxa of uncertain affinity at Rauenberg points to the need for further taxonomic studies of the flora of this time interval. Comparisons with European assemblages of the early Oligocene reveal that the vegetation diversity in Europe during this time interval is far from being well understood.

**KEYWORDS:** leaves, cuticles, taxonomy, vegetation reconstruction, Rupelian, NP 23

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## INTRODUCTION

During the early Oligocene, Earth's ecosystems adapted to cooling climatic conditions following the preceding Late Eocene thermal maximum (Zachos et al. 2008, Roth-Nebel-sick et al. 2014). In Europe, diverse floras of this period are known from the southeastern margin of the Paratethys Sea (Hungary, Tard Clay Formation; Kvaček & Hably 1998, Hably & Erdei 2015) and the northern margin of former Europe, that is, North Bohemia (Bechlejovice (Kvaček & Walther 2004), Kundratice (Kvaček & Walther 1998), Markvartice (Bůžek et al. 1976, Kvaček & Walther 2001), Suletice-Berand (Kvaček & Walther 1995)) and Saxony (Hammer-unterwiesenthal (Walther 1998), Haselbach

Serie (Mai & Walther 1978), Kleinsaubernitz (Walther 1999), and Seifhennersdorf (Walther & Kvaček 2007)).

In the Upper Rhine valley and the Mainz Basin, early Oligocene marine sediments are known for their rich fossil record. From the Mainz Basin, Kvaček (2004a) revised the plant record from marine deposits of Flörsheim, and Pross et al. (1998) studied palynomorphs (Bodenheim drill core), both NP 23, Rupelian in age. In the region around the town of Rauenberg near Wiesloch, these clay- to siltstones were mined in several clay pits. In the respective museum collections, such material is usually held under the locality name Frauenweiler, which is located in the northwestern

part of Rauenberg. This study follows the proposal of Maxwell et al. (2016) and simply summarises all material from different clay pits under Rauenberg. While fish, e.g., Micklich & Parin (1996), dinoflagellate cysts, calcareous nannoplankton and foraminifera (Grimm et al. 2002), and birds, e.g., Mayr (2004), Mayr & Micklich (2010), have been studied in detail, this is not the case for other organism groups such as molluscs, insects, reptiles, and plants. A short note on the macro-flora was published by Winterscheid & Gregor (2008). In the synthesis of the Rauenberg fossil lagerstätte, Maxwell et al. (2016) provide a comprehensive summary of all organismic groups present at Rauenberg, including a preliminary list of fossil plant taxa and the ecological implications of this flora. Since most of the plant taxa are entire-margined, a taxonomic assessment requires the application of cuticular analysis. The results of those taxonomic studies are provided in the present paper. Due to the high organismic diversity, the fossil lagerstätte of Rauenberg offers a unique insight into an early Oligocene ecosystem (Maxwell et al. 2016).

The State Museum of Natural History Stuttgart (SMNS) houses a large fossil collection from Rauenberg including plants, invertebrates (insects, molluscs, crustaceans) and vertebrates (fish, reptiles, birds). These are available thanks mainly to the private collectors Rudolf Metzler and Harald and Annette Oechsler, who have conducted fieldwork over many years. Additional material derives from museum field campaigns. The collection of fossil plants comprises over 650 slabs. In the course of this study, the respective collection in the Naturmuseum Augsburg (NMA) was also examined, which was the basis for the publication by Winterscheid & Gregor (2008), as well as the collection at the Staatliches Museum für Naturkunde Karlsruhe (SMNK). Comparative studies of the cuticle slides from the flora of Flörsheim (Kvaček 2004a) were limited because these slides are almost completely dried.

#### GEOGRAPHICAL AND GEOLOGICAL SETTING AND AGE

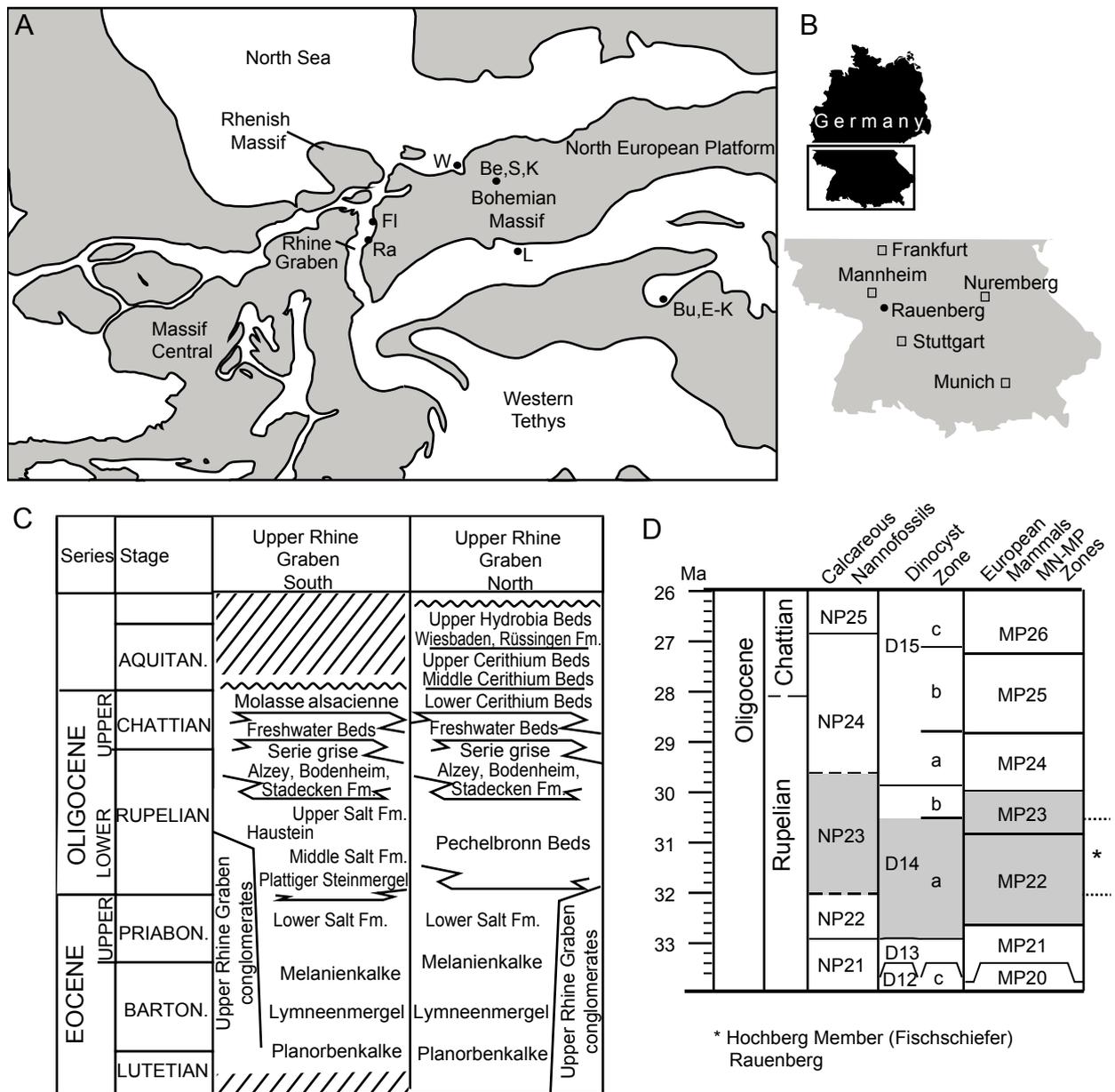
The town of Rauenberg is located 16 km south of Heidelberg, State of Baden-Württemberg, Germany, along the Upper Rhine valley.

The clay pits around Rauenberg are situated in the Upper Rhine Graben (Fig. 1), a region of intensive tectonics during the Palaeogene and Neogene and still active today. The sediments exposed in the clay pits stem from the second Rupelian transgression (Hardenbol et al. 1998). They are assigned to the marine to brackish Froidefontaine Subgroup, Bodenheimer Formation, which extends widely in the Upper Rhine Graben and its subbasins (Grimm 2005, Grimm et al. 2011). In the Rauenberg clay pits the Wallau and Hochberg Members of the Bodenheimer Formation are developed. Lithologically the sediments are partly well-bedded or laminated clay- to siltstones. Rhythmic sedimentological events and changing carbonate content resulted in lamination, among other processes. Frequent mass occurrences of calcareous nannoplankton produce laminae of calcareous mud or calcareous sand layers. Based on calcareous nannoplankton, the Hochberg Member is assigned to NP 23. Rupelian age is supported by dinoflagellate cysts and foraminifera (Grimm et al. 2002). The Alzey Formation, which is characterised by coarser sediments, represents the fully marine coastal equivalent of the Bodenheimer Formation and comprises sands and gravels (Grimm 2005). Barite concretions in these sandy sediments of the Alzey Formation bear, among other fossils, abundant remains of pine cones and wood (Mallison 2002). For detailed geology and stratigraphy see Maxwell et al. (2016).

#### MATERIALS AND METHODS

The fossil flora of Rauenberg yields mainly leaves and more rarely fructifications, as well as marine algae. The plant material is preserved mainly as carbonised compressions and is highly scattered, as is characteristic of marine sediments. Private collectors preferred to collect complete specimens rather than very fragmented ones. Such material has been collected only since 2007, when the author contacted the collectors. Little stratigraphic information is available for the collection material from private collectors. Accordingly, potential changes in composition in the geological section cannot be traced. This information has been rigorously documented only since the SMNK began field campaigns.

The plant material was studied gross morphologically and, if possible, by cuticular analysis. Unfortunately, much of the material collected prior to 2007 either is coated by varnish or has been transferred to an artificial resin, both hampering cuticle studies.



**Fig. 1.** Geography and stratigraphy. **A** – Early Oligocene (Rupelian) palaeogeography of Europe, showing important Oligocene localities discussed in the text. Map modified from Meulenkamp et al. (2000) based on Spiegel et al. (2007). **B** – Location of Rauenberg, Baden-Württemberg, Germany. **C** – Lithostratigraphy of the Upper Rhine Graben, modified after Rasser et al. (2008). **D** – Estimated biostratigraphic age of the Hochberg Member (Fischschiefer). Fl – Flörsheim, Mainz Basin; Ra – Rauenberg; S – Seiffenhensdorf; W – Weisselster Basin, Germany; Be – Bechlejovice; K – Kundratice, Czech Republic; Bu, E-K – Budapest and Eger-Kiseged, Hungary; L – Linz, Austria. Figure 1 after Maxwell et al. (2016) slightly modified

Nevertheless, cuticles were prepared from about 300 specimens, of which >200 attempts were successful. To prepare the cuticles, the samples were treated with 5–10% hydrochloric acid (HCl) followed by 10–20% hydrofluoric acid (HF) to dissolve the sediment. The leaf fragments were then macerated with Schulze’s reagent (HNO<sub>3</sub>+KClO<sub>3</sub>), followed by treatment in 5% potassium hydroxide solution (KOH). The cuticles were stained with safranin and embedded in glycerol. The cover glasses were sealed with nail polish. The cuticles of many specimens are heavily infected by fungi, often masking the stomata.

For cuticle descriptions, representative values were obtained by measuring at least three leaves per

taxon wherever possible. Ten measurements of every cell type (stomata, non-modified epidermal cells, trichome bases per leaf) were taken wherever possible. Averages refer to values per leaf. Cuticles were studied under a Leitz interference contrast microscope. SEM studies were performed on a Zeiss EVO LS 15. All cuticle slides are stored in the SMNS.

Acronyms in this study: NMA – Naturmuseum Augsburg, SMNK – Staatliches Museum für Naturkunde Karlsruhe, SMNS – State Museum of Natural History Stuttgart.

Abbreviations in descriptions: l × w for length × width, l/w ratio for ratio length/width.

## SYSTEMATIC PART

Systematics follows the Open Tree of Life (Hinchliff et al. 2015).

## FUNGI

## Microthyriaceae Sacc.

**Microthyriaceae** gen. et sp. indet.

Pl. 8, figs 1–3

Material. SMNS P 1952/473.

Description. Cylindrical spores with rounded poles and concentrically growing fruiting bodies in different stages.

Remarks. Similar spores and fruiting bodies are met frequently on fossil leaf material, e.g., Kovar (1982). In Rauenberg they occur sporadically, while hyphae of fungi are much more common. From Upper Oligocene sediments in Greenland, Worobiec and Worobiec (2013) treated similar structures taxonomically. The specimens from Rauenberg are not assigned more closely because diagnostic features are poor.

## ALGAE

## Phaeophyceae

**Cystoseirites** Sternberg**Cystoseirites communis** Unger

Pl. 1, fig. 1

1847 *Cystoseirites communis*, Unger, p. 125, pl. 38, figs 1, 2.

Material. SMNS P 1953/111.

Description. Filamentous, multiply branched thallus, filaments up to 1 mm wide, bearing elongated aerocysts of up to 4 mm length and about 1 mm width.

Remarks. The aerocysts account for the assignment to the Phaeophyceae. *Cystoseirites communis* was first described from Radočaj, Croatia (middle Miocene, Sarmatian). These algae differ from *Cystoseirites altoaustriacus* Kovar by having elongated, rather

tiny aerocysts. In marine deposits of different ages, *Cystoseirites*-type algae are sometimes frequent, for example in the surroundings of Linz, Austria, earliest Miocene (Kovar 1982), and Sarmatian deposits of Romania (Givulescu 1975, Paraschiv 2004). From Rauenberg this is the only remain; from Flörsheim (Mainz Basin) no aerocyst-bearing algae have been reported.

## Phaeophyceae vel Rhodophyceae

**Laminarites** Sternberg**Laminarites latus** Engelhardt

Pl. 1, fig. 4

2004a *Laminarites latus* Engelhardt; Kvaček, p. 3, pl. 1, figs 9, 10.

Material. SMNS P 1952/97 (together with *Platanus neptuni*), 188, 197, 199, 207, 213+214, 242, 295, 347.

Description. Fragments of thalli, band-like, straight to gently bent, parallel-sided, densely spaced strands sometimes faintly visible, up to 160 mm long, up to 17 mm wide, unbranched.

Remarks. These thalli differ from the below-described ones by their larger width and the absence of branchings. In specimen SMNS P 1952/242 the margins are darker, possibly indicating that the margin was slightly thicker.

**Thallites** Walton**Thallites multifidus** (Brongniart) Kvaček

Pl. 1, figs 2, 3

2004a *Thallites multifidus* (Brongniart) comb. nov.; Kvaček, p. 4, pl. 1, fig. 1.

Material. SMNS P 1952/1, 39, 78, 126, 131, 138, 148, 323; SMNS P 1953/104, 121, 122.

Description. Thalli (multiply) dichotomously forked, sometimes forming dense mats, branches up to 3 mm wide.

Remarks. Remains of this type are quite common. From Flörsheim one small specimen has been described bearing a close resemblance based on the few available characters.

## FERNS

## Schizaeales

## Schizaeaceae Kaulf.

*Lygodium* Sw.*Lygodium kaulfussii* Heer emend.

Gardner et Ettingshausen

Pl. 1, figs 5–7

1861 *Lygodium kaulfussi*, Heer 1861, p. 409, pl. 9, fig. 1.2004a *Lygodium kaulfusii* Heer emend. Gardner et Ettingshausen; Kvaček, p. 4, pl. 1, fig. 11.

Material. SMNS P 1952/55 (pinna), 322, 332 (isolated lobes).

Description. A single palmate pinna and two fragments; palmate pinna length  $\times$  width (hereafter  $l \times w$ ) =  $12 \times 15$  mm, base cuneate, pinna dissected into four lobes, three of them rather complete, lobes 2 mm wide, neither margin nor apices preserved; veins ascending steeply and forking, midvein vague; two isolated pinnae (i.e. lobes) both lacking base and apex,  $l \times w = 21 \times 5$  mm (SMNS P 1952/322) and  $l \times w = 19 \times 4$  mm (SMNS P 1952/332), narrow with parallel, finely crenulate/serrate margins, main vein slender, smoothly wavy, higher-order veins ascending steeply from the main vein, then turning towards the margin, course wavy, forking at least once, usually twice or even three times, ending in the marginal tooth apices.

Remarks. Compared to the records from Flörsheim (Kvaček 2004a) and Geiseltal (Eocene, Barthel 1976), this is a remarkably tiny palmate pinna. Its margin is not preserved, thus the termination of the veins remains unclarified and the pinna lacks unambiguous main veins running into the lobes. The latter fact may, however, be an artefact caused by poor preservation, whereas the isolated lobes are better preserved.

*Filicopsida* sp.

Material. SMNS P 1952/69.

Description. Fragment of pinna,  $l \times w = 9$  (incomplete)  $\times 3$  mm, with distinct midvein, further veins arising from it at about  $45^\circ$  angle or more, once or twice forking, marginal

termination ambiguous, margin dentate or crenulate, somewhat rolled into the sediment.

Remarks. This pinna fragment differs from the above-described ones by the vein pattern in which the midvein is straight and the lateral veins arise under wider angles.

## GYMNOSPERMS

## Cycadales

## Zamiaceae Reichenbach

*Ceratozamia* A. Brongniart*Ceratozamia floersheimensis*

(Engelhardt) Kvaček

Pl. 1, fig. 8; Pl. 8, figs 4–7

1911 *Iris floersheimensis* Engelhardt, p. 319, pl. 37, fig. 27.2002 *Ceratozamia floersheimensis* (Engelhardt) comb. nov.; Kvaček, p. 305, figs 1–21.2014 *Ceratozamia floersheimensis* (Engelhardt) Kvaček; Kvaček, p. 234, pl. 1, figs 6–7, pl. 2 fig. 10.

Material. SMNS P 1952/456.

Description. Fragment of a leaflet, texture coriaceous,  $l \times w = 50$  (incomplete)  $\times 8$  mm, narrow, parallel-margined, gradually tapering towards one end; venation parallel.

Micromorphology. Adaxial and abaxial cuticle thick, bearing cells of two types: (1) elongated ones, anticlines straight to somewhat bent, length very variable up to  $150 \mu\text{m}$ , width  $10\text{--}18 \mu\text{m}$ , cross-walls mainly distinctly oblique, curved or S-shaped, (2) short rows ( $100$  to at least  $150 \mu\text{m}$  long) of more strongly cutinised short cells, length variable up to  $50 \mu\text{m}$ , width  $9\text{--}13 \mu\text{m}$ , epicuticular striation to folding paralleling the cell rows; stomatal complexes confined to abaxial cuticle, mainly longitudinally oriented, mono- to di- (or tri-) cyclocytic, subsidiary cells up to 6, very variable in shape, e.g.,  $l \times w = 93 \times 71 \mu\text{m}$ ,  $114 \times 74 \mu\text{m}$ , stomata somewhat recessed, remains of guard cells occasionally still present, e.g.,  $l \times w = 40 \times 34 \mu\text{m}$ ,  $34 \times 29 \mu\text{m}$ .

Remarks. This is the fragment of a narrow cycad leaflet lacking base and apex, although it tapers at one end. It was detected among the material accessed since 2007, when collection of strongly fragmented material was encouraged

by the author. Among cycads, short, thickly cutinised cells arranged in rows are characteristic of the genus *Ceratozamia* (Kvaček 2002). Diagnostically relevant features to distinguish *C. floersheimensis* and *C. hofmannii* are few. Of these, the presence of venation forkings remains open in the specimen from Rauenberg because the fragment is rather small. The leaflet attachment also remains unclear because the base is missing. Based on cuticular features, *C. hofmannii* differs from *C. floersheimensis* by having distinctly smaller, short cells (Kvaček 2004b). In this respect, the here-described specimen clearly matches *C. floersheimensis*. Apart from Rauenberg and the type locality Flörsheim, *C. floersheimensis* is known from the Oligocene of Hungary (Budapest-Nagybátony, Tard Clay) and Slovenia (Trbovlje) (Kvaček 2002, 2014). A modern relationship exists to *C. microstrobila* Vovides & J.D. Rees, *C. morettii* Vázquez-Torres & Vovides, *C. latifolia* Miquel, and *C. delucana* Vázquez-Torres, Moretti & Carvajal-Hernández (Kvaček 2014).

Araucales/Cupressales

Doliosrobaceae Kvaček

***Doliosrobis*** Marion

***Doliosrobis taxiformis*** (Sternberg) Kvaček  
? ***taxiformis*** Mai & Walther

Pl. 1, fig. 9

1833 *Cystoseirites taxiformis*, Sternberg, fasc. 5–6, p. 35, pl. 18, figs 1–3.

1971a *Doliosrobis taxiformis* (Sternberg) comb. nov.; Kvaček, p.118, pl. 31, fig. 19, pl. 32, figs 1–5.

2008 *Doliosrobis taxiformis* (Sternberg 1833) Kvaček 1971; Winterscheid et Gregor, p. 4.

Material. NMA 2006-104/1497.

**Description.** Terminate foliated shoot, branched twice near base, 110 mm long, tapering towards apex; leaves helically arranged, basally decurrent along axis, apical part free, awl-shaped.

**Micromorphology.** Large, straight-walled non-modified epidermal cells of possibly stomata-bearing zones, presence of stomata ambiguous.

**Remarks.** For this specimen, cuticle preparation was not successful. Gross morphologically it is more similar to *Doliosrobis taxiformis* than to *Chamaecyparites hardtii* (Göppert)

Endlicher in which the needles usually appear to be less coriaceous and less regularly arranged (compare e.g., Kvaček 1971a, pl. 31, fig. 17, Kunzmann 1999, pl. 24, figs 1–4). The assignment to the variety *taxiformis*, which is characterised by larger stomata than the variety *sternbergii* (Mai & Walther 1985), remains somewhat ambiguous. Winterscheid and Gregor (2008) listed *D. taxiformis* from Rauenberg without a figure. Although the collection file number given in that publication does not correspond to the number on the specimen itself, I assume that those authors referred to this specimen for two reasons: (1) it is the only specimen in the respective collection in the Naturmuseum Augsburg that may be assigned to *Doliosrobis*; and (2) in their publication, numerous collection file numbers do not correspond to those on the specimens themselves. *Doliosrobis taxiformis* is one of the ancient taxa in this assemblage.

Cupressales

Cupressaceae

***Sequoia*** Endl.

***Sequoia abietina***

(Brongniart in Cuvier) Knobloch

Pl. 1, fig. 10; Pl. 8, fig. 8

1964 *Sequoia abietina* (Brongn. in Cuv.) Knobloch, Knobloch, p. 601.

Material. NMA 2016-3/2179.

**Description.** Foliated shoot 70 mm long, needles densely spaced, helically arranged but oriented in one plane along the twig, needles up to 11 mm long and 1.1–1.4 mm wide, entire-margined, needle width tapering towards base, twisted and somewhat decurrent along the twig, lacking a distinct petiole, apex acute acuminate.

**Micromorphology.** Non-modified epidermal cells elongate, mainly rather rectangular to oblique, arranged in rows paralleling the needle length, stomata confined to stomata bands, mainly oriented paralleling the rows of non-modified epidermal cells, stomata cyclocyclic to amphicyclic, subsidiaries more strongly cutinised than non-modified cells, well staining, polar cells smaller than lateral ones, stomatal aperture narrow oblong, 19–29 (average 26) µm long.

Remarks. Gross morphologically the needles of *Sequoia* are usually wider than those of *Taxodium*. The prevailing orientation of the stomata parallel to the needle length unequivocally confirms this assignment. This is the only specimen documenting this species at Rauenberg.

***Taxodium* Rich.**

***Taxodium* sp.**

Pl. 1, figs 11–13

Material. SMNS P 1952/88, SMNS P 1953/103. SMNK 7710.

Description. Detached shoots with longest needles in the middle part, needles helically inserted but spread in two opposite ranks, directly attached to the axis (sessile, no petiole),  $l \times w$  up to  $9 \times 1$  mm.

Remarks. The assignment to *Taxodium* is based on shoot shape, needle arrangement and needle width. Abietoid shoots of *Sequoia* are more robust and bear thicker needles. Twigs with cupressoid foliage reminiscent of *Sequoia* or *Glyptostrobus* are absent in Rauenberg. A further, poorly preserved, rather thick twig fragment shows cupressoid foliage and is assigned to the Taxodioideae. Records of the Taxodioideae are remarkably scarce in Rauenberg and are restricted to shoots.

***Tetraclinis* Mast.**

***Tetraclinis salicornioides* (Unger) Kvaček**

Pl. 1, figs 14, 15; Pl. 8, fig. 9

1841 *Thuytes salicornioides* Unger, p. 11 pl. 2 figs 1–4.

1989 *Tetraclinis salicornioides* (Unger) comb. nov. ; Kvaček, p. 48–51, pl. 1 fig. 11, pl. 2 figs 2–14, pl. 3, figs 3, 4.

2008 *Tetraclinis salicornioides* (Unger 1841) Kvaček 1989; Winterscheid & Gregor, pl. 1 fig. 2.

Material. SMNS P 1952/20, 21, 70, 118, 144, 187, 194, 198, 226, 262, 294, 300, 313, 324, 326, 417, 420, 421, 422, 428, 457; SMNS P 1953/109. NMA 2006-118/1497.

Description. Fragments of twigs, most of them consisting only of one whorl of leaves fused in four, in some specimens several whorls still attached to each other, remains of branched twigs exceptional; whorl length

usually less than 10 mm; specimen SMNS P 1953/109 a twig fragment consisting of four whorls about 15 mm long and branching buds.

Micromorphology. Cuticle thick, anticlines of non-modified epidermal cells distinct, undulate with knobs, forming quadrangular cells in non-stomatal areas and more irregular polygonal cells in stomatal areas, often one or two papillae (strongly cutinised regions) on the surface of the non-modified epidermal cells, very variable in size, quadrangular cells up to 50  $\mu\text{m}$  in length, polygonal cells 25–40  $\mu\text{m}$  in diameter, stomatal complexes partly incompletely amphicyclocytic, adjacent stomata sometimes sharing subsidiary cells, aperture bordered by a thick, rather quadrangular Florin-ring, aperture diameter 6–12  $\mu\text{m}$ .

Remarks. The true organisation of the leaf arrangement, namely four leaves in one whorl (not decussate) and marginally adnate, was recognised by Kovar (1982), although she hesitated to assign these remains to *Tetraclinis*. The twig SMNS P 1953/109, reminiscent of *T. brachyodon* (Brongniart) Mai & Walther (pl. 1, fig. 15), is assigned to *T. salicornioides* because different positions on the living plant may have been reflected in morphological variability.

Pinales

Pinaceae Lindl.

***Pinus* L.**

***Pinus (Strobus) sp. 1***

Pl. 1, fig. 16

Material. SMNS P 1952/292. ? SMNK 7747.

Description. Five-needled fascicle, needles 33 mm long, complete, slender, with a central keel, apex acute.

Remarks. Though the sheath is hardly preserved, this remain corresponds very well with the single fascicle of *P. (Strobus) sp.* described from Flörsheim by Kvaček (2004a).

***Pinus (Strobus) sp. 2***

Pl. 1, fig. 17

Material. SMNS P 1952/89+90, ? 91, 248.

**Description.** Five-needled fascicles, needles 72 mm (SMNS P 1952/89+90) to 89 mm (SMNS P 1952/248) long, slender, with a central keel, apex acute.

**Remarks.** These fascicles differ from the foregoing species by having distinctly longer needles. In specimen SMNS P 1952/248, four needles are visible, and in specimen SMNS P 1952/91 only three; the others probably are covered by sediment.

### *Pinus* sp. 3

Pl. 1, fig. 18

**Material.** SMNS P 1952/92, 460. NMA 2006-103/1497.

**Description.** Two-needled fascicles, up to 115 mm long, up to 1 mm wide, rigid, apex ?, sheath up to ? 5 mm long.

**Remarks.** The needles appear to be rather delicate but stiff.

### *Pinus* sp. 4

Pl. 1, fig. 19

**Material.** SMNS P 1952/143.

**Description.** Pair of needles 155 mm long (incomplete), 1.5 mm wide, base and apex incomplete, needles gently bent.

**Remarks.** This species differs from the foregoing one by its broader and probably longer needles.

### *Pinus* sp. 5

2008 *Pinus* sp. – zweinadelige Belaubung; Winterscheid & Gregor, p. 4, pl. 1, fig. 1.

**Material.** NMA 2006-101/1497, 2006-102/1497.

**Description.** Two-needled fascicles, needle length 72 mm (complete)–80 mm or somewhat more.

**Remarks.** This species differs from *Pinus* spp. 3 and 4 by having shorter needles. Specimen NMA 2006-101/1497 has been figured by Winterscheid and Gregor (2008, pl. 1 fig. 1) under an incorrect inventory number: 2006-184/1497.

### *Pinus* sp. 6

Pl. 1, fig. 20

2008 *Pinus* sp. – dreinadelige Belaubung; Winterscheid & Gregor, p. 4.

**Material.** NMA 2006-111/1497.

**Description.** Single, almost complete, three-needled fascicle, full needle length 66 mm.

**Remarks.** This is the only record of a three-needled pine species.

### *Pinus engelhardtii* Menzel

Pl. 3, fig. 10

**Material.** SMNK 7706.

**Description.** Slender elliptic cone,  $l \times w = 83$  (? 85–90)  $\times$  about 40 mm, cone scales curved strongly outwards, apophyses narrow-rhomboidal, with short umbo and mucro.

**Remarks.** This cone differs markedly from the below-described ones by its distinctly recurved cone scales with narrow apophyses.

### *Pinus (Pinus) cf. thomasiana*

(Goeppert) Reichenbach

Pl. 3, figs 11, 12

2002 *Pinus nodosa* Ludwig; Mallison, p. 19, pl. 3 figs 6–8.

2004a ? *Pinus (Pinus) cf. thomasiana* (Goeppert) Reichenbach; Kvaček, p. 6, pl. 3 figs 10, 11, 13.

**Material.** SMNS P 1952/? 48, 176; SMNS P 1953/106, 110.

**Description.** Broad conical cones,  $l \times w = 40$ –60  $\times$  28–37 mm, petiole adherent, cone scales thick, apophyses rather flat, rhomboidal, wider than high, with medial keel, (ex)centromucronate; towards cone apex, keel and umbo shifting towards top of the apophyses.

**Remarks.** These specimens have been embedded by transfer technique in artificial resin. It is likely that specimens SMNS P 1952/176 and SMNS P 1953/110 represent part and counterpart shared between the private collectors and later placed in the collection of the SMNS. In all specimens the apophyses are rather flat, as is characteristic for *Pinus hampeana*, which is known only from the Miocene. The Palaeogene species *P. thomasiana* (Goeppert) Reichenbach bears a resemblance, but the apophyses are

domed, whereas they are relatively flat in our specimens. Whether this state is an artefact due to diagenetic processes remains unclear.

From baryth concretions of the Alzey Formation, *Pinus nodosa* Ludwig (Mallison 2002) resembles the here-described pine cones, although details of the apophyses and umbo are less distinctly preserved in these specimens.

Concluding from the assignment, the pine cones from Flörsheim were also clearly difficult to determine (Kvaček 2004a). *P. thomasi-ana* is assigned to section *Sylvestres* Van der Burgh, Series *Nigrae* Novák, showing close affinities especially to modern *P. nigra* Arnold and *P. heldreichii* Christ (Mai 1986).

## ANGIOSPERMS

### Laurales

#### Lauraceae Juss.

#### *Actinodaphne* Nees

##### *Actinodaphne pseudogermari*

Walther in Mai & Walther 1985

Pl. 2, fig. 26; Pl. 9, figs 1–3

1985 *Actinodaphne pseudogermari* Walther nov. spec.; Mai & Walther, p. 33, pl. 22, figs 1–4, Bild 1/12–15, Bild 13/3–4.

2002 *Actinodaphne pseudogermari* Walther in Mai & Walther, 1985; Kunzmann & Walther, p. 266, figs 4a, g, 5d, e.

Material. SMNS P 1952/17.

**Description.** Fragment of a leaf base with a short and swollen petiole, midvein prominent, petiole and midvein with distinct wrinkles parallel to the leaf axis, laminar shape ambiguous, base angle acute, base straight but convex directly above the petiole and somewhat asymmetric;  $l \times w = 65$  (? 120)  $\times$  25 (? 26–27) mm, entire-margined, secondary veins arising at an angle of up to 45°.

**Micromorphology.** Adaxial and abaxial cuticles thick, glabrous; adaxial cuticle: anticlines very thick, curved to somewhat wavy, non-modified cells 17–26 (average 22)  $\mu\text{m}$  across; abaxial cuticle: anticlines distinct but less thick than adaxially, straight to curved, size of non-modified cells 17–23 (average 21)  $\mu\text{m}$ , stomatal complexes brachyparacytic,

asymmetric, stomata sunken, stoma  $l \times w = 15$ –19 (average 17)  $\times$  12–18 (average 14)  $\mu\text{m}$ , stomatal aperture narrow, slit-like, ledges somewhat thickened, pore short, mesophyllous oil cells abundant, variable in size (7–66  $\mu\text{m}$ ).

**Remarks.** The complete size of the here-described specimen can be only roughly estimated. Trichome bases have not been observed. The stomata may resemble *Actinodaphne pseudogermari* Walther & Kvaček and *Laurophyllum acutimontanum* Mai. In *L. meuselii* the stomata are somewhat diffusely overlapped by the delicate surface of the adjacent cells, while in *A. pseudogermari* the overlap is sharply delimited. *L. acutimontanum* differs both from *A. pseudogermari* and *L. meuselii* by its mostly stronger overlap of the stomata by domed cells leaving a rather narrow, irregularly slit-like opening above the stoma. The margins of the central opening appear somewhat thickened, unlike *L. meuselii*. Previously, *A. pseudogermari* was known only from the Upper Eocene.

#### *Daphnogene* Unger

##### *Daphnogene cinnamomifolia*

(Brongniart) Unger

Pl. 2 figs 1–6; Pl. 9 figs 4–9

2002 *Daphnogene cinnamomifolia* (Brongniart) Unger; Mallison p. 39, pl. 9, figs 3, 4.

2004a *Daphnogene cinnamomifolia* (Brongniart) Unger; Kvaček, p. 9, pl. 6, figs 10–14, pl. 7, figs 7–9.

2008 *Daphnogene cinnamomifolia* (Brongniart in Cuvier 1822) Unger 1850; Winterscheid & Gregor, p. 4.

Material. SMNS P 1952/ 8, 13, 15, 24 B, 38, 49, 51, 60, 64, 68, 71, 76, 77, 116, 121, 136, 140, 164, cf. 165, 174, 182, 185, 227, 228, 260, 261, 267, 273, 279, 296, 303, 314, 319, 320, 328, 331, 357, 358, 364, 415?, 418, 423, 425–427, 430, 432, 449, 450, 451, 453, 455, 466, 471, 472; SMNS P 1953/1–14, 16–19, 21, 22, 49, 69, 76.

**Description.** Petiolate, entire-margined leaves, texture coriaceous, petiole up to 20 mm long, laminar shape oblong to elliptic or somewhat ovate,  $l \times w = 19$ –110  $\times$  7–47 mm,  $l/w$  ratio = 2.2–5.6, base straight to somewhat rounded, base angle acute, apex straight to acuminate, apex angle acute; midvein straight,

basal secondaries suboppositely suprabasal acrodromous, usually prominent, running onto upper third of the lamina, further secondaries distinctly weaker, arising at angles of about 40–50° in broader leaves and narrower angles in smaller ones, such secondaries being restricted to the upper part of the lamina, brochidodromous, abmedially looping veinlets arising from suprabasal secondaries, tertiaries (mainly hardly visible) percurrent.

**Micromorphology.** Adaxial cuticle thick, anticlines of non-modified cells distinct, from almost straight or curved to moderately undulate, cells 15–38 (20–31) µm across, largely glabrous to trichome bases rather densely spaced; abaxial cuticle delicate, in larger leaves more delicate than in smaller ones, anticlines of non-modified cells delicate, rounded to undulate with smaller amplitude and wave length than adaxially, cells 12–35 (16–20) µm across, stomatal complexes brachyparacytic, oval to rhomboidal, often asymmetric, weakly staining, subsidiaries not offset from guard cells, aperture very short, slit-like, stoma length 10–20 (14–17) µm; trichome bases scattered to dense, considerably variable in shape and size, either situated in the plane of the cuticle or raised above the cuticle surface, trichome pore slit-like or a roundish pore 6–13 µm in diameter, sometimes with a thickened poral rim, encircling cells ± distinct, intensively staining and ± radially elongated; globular mesophyllous secretory bodies sometimes preserved.

**Remarks.** Variability of trichome density and of the undulation of the anticlines both adaxially and abaxially, largely going along with variability of leaf size, have been explained repeatedly as an expression of the leaf position on the living plant, that is, by whether they are sun or shade leaves, e.g., Kvaček & Walther (1978). Sometimes presumable shade leaves are described as forma *lanceolata* and sun leaves as forma *cinnamomifolia*, e.g., Walther (1999). Due to morphological overlaps, this distinction is not applied here.

Trichome base variability (bases raised above surface or not, shape of encircling cells, shape and size of trichome pore, presence of distinct poral rim) has not yet been examined in terms of its taxonomic value. Specimen SMNS P 1953/76 is distinct due to the thick poral rim of the trichome pore (pl. 9, fig. 6), while the other cuticular features match *Daphnogene*

very well. This specimen resembles *Laurophyllum* sp. 2 (Winterscheid & Kvaček 2014, pl. 9 fig. 12). Since the species diversity of *Daphnogene*-like foliage is still unresolved, the characteristics of the indumentum may help differentiate fossil species.

*Daphnogene cinnamomifolia* is among the most common species in Rauenberg. Unlike at Flörsheim, no fragmentary twig has been recovered. The variability of laminar size is very similar in both localities (Flörsheim 1 × w = 50–120 × 10–53 mm, Rauenberg 19–110 × 7–47 mm).

### *Laurus* L.

#### *Laurus abchasica*

(Kolakovskii & Shakryl) Ferguson

Pl. 6, figs 11–13; Pl. 10, figs 1–3

- 1958 *Laurophyllum abchasicum*, Kolakovskii & Shakryl in Kolakovskii, p. 346, pl. 7, figs 1–3, pl. 10, figs 4–8.  
 1974 *Laurus abchasica* (Kolakovskii & Shakryl) comb. nov.; Ferguson, p. 64, figs 7A–H, 8A–D, 9A–D, 10.  
 2004a *Laurus abchasica* (Kolakovskii & Shakryl) Ferguson; Kvaček, p. 6, pl. 4, figs 1, 2, pl. 5, figs 1–3.

**Material.** SMNS P 1952/268, 377, 382; SMNS P 1953/65, 75.

**Description.** One almost complete leaf and fragments of narrow elliptic, entire-margined leaves, 1 × w up to 96 (about 120) × 22 mm, base ?acute, apex angle acute, apex shape almost straight to somewhat acuminate, texture moderately firm.

**Micromorphology.** Cuticles of both sides moderately thick, largely glabrous, anticlines of non-modified epidermal cells strongly zig-zag undulate, undulation moderately deep, bead-like thickenings at tips of lobes, cells of similar size on both sides 15–44 (average 25–32) µm across, SMNS P 1953/65 with hypodermis adaxially; abaxial cuticle: stomatal complexes paracytic, shape roundish to rhomboidal, guard cells and subsidiary cells hardly staining and hardly delimited from each other, stomatal complexes 1 × w = 16–26 (average 18–21) µm × 13–28 (average 18–22) µm, l/w ratio = 0.6–1.5 (average 0.9–1.1), stomatal aperture spindle-shaped, ledges slightly thickened, aperture length 5–16 (average 9–12) µm.

**Remarks.** A single leaf (SMNS P 1953/75) is

almost complete. The largest leaf whose apical half is preserved probably measured about 110 mm in length and 22 mm in width. The cuticular structure of these remains clearly points towards *Laurus abchasica*. *Laurophyllum fischkandelii* Kunzmann et Walther (2002) is described from the late Eocene of the Weißelster Basin; it differs by its very narrow and strongly omega-like undulation of the anticlines both adaxially and abaxially. Remarkable is the presence of a hypodermis on specimen SMNS P 1953/65 from Rauenberg. Ferguson (1971) describes for taxon XXIII from Kreuzau, which corresponds to *Laurus abchasica*, “primary cells often subdivided by secondary cell walls” on the adaxial cuticle, but does not mention whether this refers to a hypodermis. *L. abchasica* records are more common during the late Oligocene and the subsequent Miocene than in the early Oligocene. Apart from two leaves recorded from Flörsheim (Kvaček 2004a), Rauenberg is the second early Oligocene record.

### *Laurophyllum* Goeppert

#### *Laurophyllum kinkelinii* (Engelhardt) Kvaček

Pl. 2, figs 7, 8; Pl. 11, figs 5–9

2004a *Laurophyllum kinkelinii* (Engelhardt) Kvaček comb. n.; Kvaček, p. 7, pl. 4, figs 10–12, pl. 5, figs 10–12.

**Material.** SMNS P 1952/184, 275+276 (part and counterpart); SMNS P 1953/64.

**Description.** Entire-margined leaves moderately coriaceous, petiole up to 15 mm long at least, laminar shape (narrow) elliptic, oblong,  $l \times w =$  up to at least  $120 \times 18$ – $25$  mm,  $l/w$  ratio about 4.8–6.7, leaf base narrow acute, apex not preserved; midvein stout, mainly straight, secondaries vaguely visible, rather widely spaced, curved.

**Micromorphology.** Adaxial cuticle thick, well preserved, anticlines distinct, smooth, straight, curved to shallow undulate with wide wave length, non-modified cells 19–41 (31, 31)  $\mu\text{m}$  across, largely glabrous, epicuticular striae mainly above veins and near margin, radial striae around trichome bases; abaxial cuticle delicate, non-modified cells domed, anticlines therefore often difficult to trace, 12–24 (18, 21)  $\mu\text{m}$  across, stomatal complexes paracytic,

stomata overlapped by subsidiaries, stomatal aperture narrow spindle-shaped to narrow elliptic to slit-like, ledges not very pronounced, stoma length 16–25 (18, 19)  $\mu\text{m}$ , trichome bases common, indistinct; mesophyllous secretory bodies rare.

**Remarks.** While specimens SMNS P 1952/275+276 and SMNS P 1953/64 are fragments of large, probably narrow elliptic leaves, SMNS P 1952/184 is a long, narrow elongate fragment. These remains differ from the below-described *Laurophyllum rauenbergense* by their bigger leaf size, less coriaceous lamina, distinctly bigger cells of the adaxial cuticle and dense spacing of the trichome bases abaxially. Unlike *L. kinkelinii* from Flörsheim, these specimens lack dense mesophyllous secretory bodies. It remains open whether this is an artefact caused by preservation or cuticle preparation. The close similarities to *L. saxonicum* Litke and *L. medimontanum* Kvaček have been pointed out by Kvaček (2004a), as was a possible relationship of *L. kinkelinii* to *Persea*.

#### *Laurophyllum* cf. *kinkelinii* (Engelhardt) Kvaček 2004 var. *glabrum* Kvaček

Pl. 2, figs 9–11; Pl. 12, figs 1–4

2004a *Laurophyllum kinkelinii* (Engelhardt) Kvaček comb. n. var. *glabrum* Kvaček var. n.; Kvaček, p. 7, pl. 4, figs 13–16, pl. 7, figs 1–3.

**Material.** SMNS P 1952/378, 396; SMNS P 1953/87.

**Description.** Macromorphology very similar to *L. kinkelinii*;  $l \times w = 53$  (? 65)– $62$  (? 90)  $\times$  15–19 mm,  $l/w$  ratio about 3.2–6.7.

**Micromorphology** also very similar to *L. kinkelinii* except for: adaxially, anticlines slightly undulate, non-modified cells 22–45 (33–37)  $\mu\text{m}$  across, striation upon veins and radial striae near rare trichome bases; abaxially scattered large trichome bases with distinct radial striation; mesophyllous secretory bodies present.

**Remarks.** SMNS P 1952/396 and SMNS P 1953/87 are medium-sized, elliptic specimens ( $l/w$  ratio about 3.2 and 4), while specimen SMNS P 1952/378 is somewhat larger and more elongated ( $l/w$  ratio about 6.7). These leaves show larger cells with somewhat undulate anticlines on the adaxial cuticle as compared to *L. kinkelinii*. They differ from the Flörsheim

material by the striae adaxially and abaxially and the lower frequency of mesophyllous secretory cells.

***Laurophyllum pseudoprinceps***

Weyland & Kilpper s.l.

Pl. 2, figs 12–16; Pl. 12, figs 5–7

- 1963 *Laurophyllum pseudoprinceps* n. sp.; Weyland & Kilpper, p. 23, figs 14–19, textfig. 6.  
 1971b *Laurophyllum pseudoprinceps* Weyland & Kilpper; Kvaček, p. 50, pl. 1, figs 4–6, pl. 3, figs 3–5, pl. 4, figs 1–4, text-fig. 1.  
 2004a *Laurophyllum pseudoprinceps* Weyland & Kilpper s.l.; Kvaček, p. 8, pl. 4 figs 3–5, pl. 5, figs 7–9.

Material. SMNS P 1952/22+27, 30+31, ?217, 265, 270, 282, 302, 312, 344, 345, 362, 365, 389, 392, 403, 409, 412, 446; SMNS P 1953/15A, 48, 84.

Description. Fragments of coriaceous leaves, rarely almost complete, laminar shape elliptic to narrow elliptic,  $l \times w = 40\text{--}85 \times 10\text{--}28$  mm,  $l/w$  ratio = 2.3–4.3, base angle (narrow) acute, base mainly cuneate, sometimes slightly convex or wavy, petiole complete in specimen SMNS P 1952/312: 10 mm long, straight, widened at base; apex angle (narrow) acute, apex mainly straight to somewhat acuminate, margin entire, sometimes line-like thickened, midvein straight, secondaries only rarely visible, basal ones sometimes more prominent.

Micromorphology. Adaxial and abaxial cuticles thick, largely glabrous, anticlines variable from almost straight to undulate, often pitted, especially adaxially; non-modified epidermal cells 15–32 (average 18–24)  $\mu\text{m}$  across adaxially; abaxial cuticle: non-modified epidermal cells 16–36 (average 23–30)  $\mu\text{m}$  across, stomatal complexes paracytic, often asymmetric, butterfly-like in shape due to the presence of big lateral subsidiary cells bordering the sunken guard cells, stomatal ledges thick, stomata length 17–27 (average 20–23)  $\mu\text{m}$ , specimen SMNS P 1953/15 stoma length 20–33 (average 24)  $\mu\text{m}$ ; mesophyllous oil cells present.

Remarks. The stoma length of the type material of *Laurophyllum pseudoprinceps* is indicated as “meist zwischen 17 und 21  $\mu$ ” (Weyland & Kilpper 1963). Kvaček (1971b) characterises the stoma length of *L. pseudoprinceps* as 17–25  $\mu\text{m}$ . *Ocotea hradekensis* resembles

*L. pseudoprinceps* strongly except for the larger stomata 25–30 (–35)  $\mu\text{m}$  (Kvaček & Bůžek 1966, Bůžek et al. 1996). This species has also been reported from Markvartice although without measurements (Bůžek et al. 1976), from Hradek nad Nísou (Holý et al. 2012), from the Cypris Shale (Bůžek et al. 1996) and from the Oder 2a lignite mine (Knobloch & Kvaček 1976) with the following variability in stoma length: 25–30 (36)  $\mu\text{m}$  (Hradek), (20–) 23–27 (–30)  $\mu\text{m}$  (Cypris Shale), and (22–) 27–30 (34) (Oder 2a). For *L. pseudoprinceps* from Flörsheim, Kvaček (2004a) describes the stomata as 22–25 (–30)  $\mu\text{m}$  long. This brief enumeration points to the difficulties of separating the two species based on stoma length. All specimens from Rauenberg included in *L. pseudoprinceps* bear stomata with an average length from 20–23  $\mu\text{m}$ , larger than that described for the type material of *L. pseudoprinceps* by Weyland & Kilpper (1963). However, they well match the stoma size of *L. pseudoprinceps* given by Kvaček (1971b). Only in specimen SMNS P 1953/15 are the stomata somewhat longer: 20–33  $\mu\text{m}$  (average length 24  $\mu\text{m}$ ). Thus it remains disputable whether this single specimen should be better assigned to *Ocotea hradekensis*.

***Laurophyllum rauenbergense***

Kovar-Eder sp. nov.

Pl. 2, figs 17–25; Pl. 10, figs 4–9

- 2004a *Laurophyllum* cf. *villense* (Weyland & Kilpper) Kvaček; Kvaček, p. 8, pl. 6, figs 1–7, pl. 7, figs 4–6.

Holotype designated here. SMNS P 1953/82.

Paratypes. SMNS P 1952/93, 391, 445; SMNS P 1953/47, 73, 85.

Stratum typicum. Bodenheim Formation, Hochberg Member, “Fischschiefer”, NP 23, early Oligocene.

Locus typicus. Rauenberg, Baden-Württemberg, Germany.

Derivatio nominis. Referring to the town of Rauenberg, where the fossil outcrop is located.

Additional material. SMNS P 1952/278, 350, 379, 395, 397. Cf.: SMNS P 1952/231, P 1953/59.

Based on gross morphology only. SMNS P 1953/91,? 94.

**Differential diagnosis.** Differing from *L. villense* (Weyland & Kilpper) Kvaček by its short stomata and absence of striae, and from *L. kinkelinii* by its smaller, non-modified epidermal cells of the adaxial cuticle.

**Description.** Rather small, narrow, entire-margined, coriaceous leaves; petiole up to 16 mm long, laminar shape oblong to somewhat ovate or minimally elliptic,  $l \times w = 35\text{--}72\text{--} ?120 \times 7\text{--}10$  mm, exceptionally up to 13 mm,  $l/w$  ratio = 4.4–9.2, base cuneate to decurrent, base angle narrow acute, base straight to somewhat convex, midvein stout, mainly straight, secondaries not visible.

**Micromorphology.** Adaxial cuticle: thickness variable, moderately thick or thick, anticlines slender to thick, sometimes knobby, mostly straight to curved, non-modified cells 9–30 (13–24)  $\mu\text{m}$  across, in specimens SMNS P 1952/391 and SMNS P 1953/82 domed, mainly glabrous; abaxial cuticle: delicate, non-modified cells domed or almost undomed, often difficult to trace, 11–33 (19–27)  $\mu\text{m}$  across, stomatal complexes paracytic, stoma shape variable due to subsidiaries which partly cover guard cells, aperture narrow, slit-like, stomatal ledges unpronounced, stoma length 12–21 (14–18)  $\mu\text{m}$ , trichome bases indistinct, rare to almost glabrous; mesophyllous secretory bodies present.

**Remarks.** This Lauraceae is characterised by its small, linear to narrow ovate and oblong leaves. The length/width ratio of the lamina is usually  $>5$ . In Flörsheim this laurel is even more common than *Daphnogene* foliage. Kvaček (2004a) hesitated about the unambiguous assignment to *Laurophyllum villense*, probably due to the cuticular striation (Weyland & Kilpper 1963) and the younger age of the type material of *L. villense*. More relevant is the difference in stoma length, which is shorter and very similar in Flörsheim (16–20  $\mu\text{m}$ , Kvaček 2004a) and Rauenberg (12–21 (average 14–18)  $\mu\text{m}$ ) as compared to *L. villense* (up to 28  $\mu\text{m}$ , Weyland & Kilpper 1963).

The assignment of the specimens SMNS P 1952/231 and SMNS P 1953/59, which match well the gross morphology of *L. rauenbergense*, is somewhat ambiguous because the stomata are less masked by the subsidiary cells.

Furthermore, specimen SMNS P 1952/231 bears rare trichome bases both adaxially and abaxially, with faint radial striation around the trichome base, which could point towards *L. kinkelinii* var. *glabrum* (see above). In the latter species, however, the cells of the adaxial epidermis are distinctly bigger than in *L. rauenbergense*. Moreover, leaves larger than typical *L. rauenbergense* forms are sometimes difficult to assign unambiguously to either *L. rauenbergense* or *L. kinkelinii* (see also Kvaček 2004a).

### ***Laurophyllum* sp. A**

Pl. 6, fig. 8; Pl. 12, figs 8, 9

**Material.** SMNS P 1952/336.

**Description.** Almost complete, entire-margined leaf, laminar shape elliptic,  $l \times w = 67$  (? 72)  $\times$  29 mm,  $l/w$  ratio about 2.5, base angle acute, base almost straight to weakly ? obtuse, apex angle acute, apex acuminate, secondaries prominently (supra)basal acrodromous.

**Micromorphology.** Adaxial and abaxial cuticle thick, non-modified epidermal cells on both sides very similar, anticlines straight, thick, cell size adaxially 15–22 (average 18)  $\mu\text{m}$ , abaxially 14–26 (average 20)  $\mu\text{m}$ ; abaxial cuticle: stomatal complexes paracytic, subsidiary cells resembling the non-modified epidermal cells in shape and size, stoma length 12–18 (average 15)  $\mu\text{m}$ , (stoma width unclear), aperture indicated by short, thickened ledges, aperture length 5–10 (average 7)  $\mu\text{m}$ ; mesophyllous oil cells present.

**Remarks.** Based on gross morphology this leaf coincides with *Daphnogene cinnamomifolia*. It differs distinctly by having a thick abaxial cuticle and prominent anticlines. The stomatal complexes are neither rhomboidal nor asymmetric, and they stain as well as the other cells. The assignment among the Lauraceae is supported by mesophyllous oil cells.

### ***Laurophyllum* sp. B**

Pl. 6, fig. 9; Pl. 13, figs 1–3

**Material.** SMNS P 1952/47.

**Description.** Basal part of a coriaceous leaf, base angle acute, base probably decurrent; petiole 14 mm long, fragmentary, lamina

$l \times w = 70$  (?  $140$ )  $\times$   $15$  (?) mm, midvein distinctly bent, base probably entire-margined.

**Micromorphology:** Adaxial and abaxial cuticle well preserved, both distinctly granular, adaxial one thicker than abaxial one, anticlines straight to somewhat curved, thicker adaxially than abaxially, non-modified cells 18–31 (abaxially 26, adaxially 24)  $\mu\text{m}$  across, glabrous; large mesophyllous oil glands present, e.g., 34  $\mu\text{m}$  in diameter; abaxial cuticle: stomatal complexes brachyparacytic, subsidiary cells sickle-shaped, not or hardly offset from guard cells, guard cells sunken, aperture slit-like, ledges slender lines, stoma length 11–23 (18)  $\mu\text{m}$ , aperture length 6–12 (9)  $\mu\text{m}$ .

**Remarks.** This leaf may belong to *Daphnogene* because it is possible that the suprabasal acrodromous secondaries are masked due to fragmentary preservation. The stomatal complexes resemble those of *Daphnogene* but are relatively well cutinised and larger. The relatively robust abaxial cuticle and the granular structure of both surfaces are further details pointing towards a different systematic position within the Lauraceae.

### *Laurophyllum* sp. C

Pl. 6, fig. 10; Pl. 13, fig. 4

**Material.** SMNS P 1953/81.

**Description.** Narrow oblong, entire-margined leaf, texture firm,  $l \times w = 65 \times 8$  mm,  $l/w$  ratio = 5.9, base and apex attenuate, petiole 5 mm (incomplete), curved; midvein straight, secondaries weakly brochidodromous, widely spaced, ascending under steep angles (about  $30^\circ$ ) and somewhat bent.

**Micromorphology.** Adaxial cuticle well cutinised, anticlines slender, smooth, widely undulate, non-modified cells 16–48 (average 29)  $\mu\text{m}$  across; abaxial cuticle poorly preserved, only stomata discernable, stomata sunken, 13–16 (average 15)  $\mu\text{m}$  long, only the area close to aperture visible, slender ledges marking the narrow aperture; both sides glabrous.

**Remarks.** There is no doubt about the family assignment of this leaf. Gross morphologically it resembles *Laurophyllum rauenbergense*, but the adaxial cuticle is more reminiscent of *L. kinkelinii*. The stomata are small even for *L. rauenbergense*.

## Arecales

### Areceaceae Schultz

#### *Palmacites* Brongniart

##### *Palmacites lamanonis* Brongniart

Pl. 3, figs 1, 2; Pl. 13, fig. 5

1822 *Palmacites lamanonis*, Brongniart, p. 38, pl. 3, fig. 1.

2004a *Palmacites lamanonis* Brongniart; Kvaček, p. 23, pl. 20, figs 1, 2.

2008 *Trachycarpus (Flabellaria) raphifolia* (Sternberg) Takhtajan; Winterscheid & Gregor, pl. 2, fig. 2.

**Material.** SMNS P 1952/66, 74, 75, 95, 96, 111, 112, 113, ? 122, 129, 175, 280; SMNS P 1953/113+114, 124.

**Description.** Fragments of fan-shaped leaves, lamina plicate, petiole unarmed, hardly extending into the lamina; specimen SMNS P 1953/124 most complete, petiole  $l \times w = 112 \times 33$  mm (incomplete), fragment of lamina 225 mm long, 20 mm wide.

**Micromorphology.** Cuticle moderately coriaceous, ?hypostomatic, adaxial cuticle: anticlines irregularly thick, areas with irregularly shaped cells, 12–25 (average 16)  $\mu\text{m}$  across, alternating with narrow elongated cells with striae; abaxial cuticle in stoma-bearing condition: anticlines regularly slender, straight to somewhat curved, cells  $\pm$  elongated to shorter than wide, cross walls mainly oblique,  $l \times w = 10\text{--}15$  (average 13)  $\times$   $5\text{--}11$  (average 7)  $\mu\text{m}$ , stomatal complexes loosely spaced, brachyparacetracytic, guard cells often indistinct and masked by fungi, ledges thickened, stomata  $l \times w = 14\text{--}20 \times 10\text{--}18$   $\mu\text{m}$  ( $n = 3$ ).

**Remarks.** According to the pragmatic classification provided by Read and Hickey (1972), these leaves match the fossil genus *Palmacites*, unlike those described below. The cuticle does not allow further systematic assignment (compare Mai & Walther 1978). Fragments of fan palms lacking a costa are more common in Rauenberg than in Flörsheim (Kvaček 2004a).

#### *Sabalites* Saporta

##### *Sabalites major* (Unger) Saporta

Pl. 3, figs 3, 4

1847 *Flabellaria major*, Unger, p. 42, pl. 14, fig. 2.

1865 *Sabalites major* (F. Unger) G. Saporta, p. 83, pl. 2.

Material. SMNS P 1952/23, 132, 169, 173; SMNS P 1953/115.

Description. Fragments of costapalmate leaves, lamina plicate, petiole unarmed, hastula acuminate-attenuate; most complete specimen (SMNS P 1952/169): petiole incomplete,  $l \times w = 105 \text{ mm} \times 35 \text{ mm}$ , fragment of fan-shaped lamina 225 mm long, 145 mm wide, hastula extending about 100 mm into the lamina.

Remarks. These palm leaves differ from those described above by having the hastula extending considerably into the lamina. In modern palms, hastulas may be very differently expressed adaxially and abaxially in one and the same species (Dransfield et al. 2008). Therefore it cannot be ruled out that these leaves represent the abaxial side of the above-described taxon *Palmacites lamanonis*.

### *Phoenicites* Brongniart

#### *Phoenicites* sp.

Pl. 3, figs 7–9; Pl. 5, fig. 1; Pl. 13, fig. 9

2004a ? *Phoenicites* sp.; Kvaček, p. 23, pl. 20, figs 3, 4.  
2008 *Phoenicites* sp.; Winterscheid & Gregor, pl. 2, fig. 1.

Material. SMNS P 1952/12, 141, 473; SMNS P 1953/116. SMNK 7793. NMA 2006-112/1497, 2006-180/1497.

Description. Fragments of pinnately dissected foliage; pinnae suboppositely arranged, rhachis up to 11 mm wide; most complete fragment of a rhachis 178 mm long (NMA 2006-112/1497), pinnae plicate, narrowing into cuneate base, divided into two unequally wide segments, longest pinna fragment 140 mm, venation very fine, densely parallel.

Micromorphology. Cuticle very delicate, cell outlines often indistinct, in non-stomatal regions anticlines straight or somewhat curved, otherwise shallow undulate, cell outlines rectangular to oblique, arranged in rows, 12–16  $\mu\text{m}$  long and 5–7  $\mu\text{m}$  wide ( $n=6$ ); stomatal complexes in bands, rather widely spaced, oriented parallel to the pinna axis, paratracytic, number of lateral subsidiary cells obscure, guard cells weakly cutinised, stomata small, 14–22 (average 16)  $\mu\text{m}$  long, front cavity wide elliptic, 8–10  $\mu\text{m}$  long ( $n=5$ ), cuticular ledges distinct, their ends not meeting each other, aperture spindle-shaped.

Remarks. The most complete specimen is that figured by Winterscheid and Gregor (2008: pl. 2 fig. 1), which is on exhibit in NMA. Other more complete specimens (SMNS P 1953/116, NMA 2006-112/1497) have been embedded by transfer technique in artificial resin. Although this hampers cuticle studies, the method prevented the specimens from falling apart.

The other specimens are far less complete. SMNS P 1952/12 is an axis with the very basal parts of the pinnae preserved only; it is the only one with cuticle preservation. In SMNS P 1952/141, the rhachis is more slender and the subdivision of the pinnae is well visible. The material at hand does not allow determination of whether the segmentation of the pinnae is of diagnostic value. A single similar specimen has also been described from Flörsheim (Kvaček 2004a). Though the segmentation of the pinnae is not mentioned there, the close-up view in pl. 20 fig. 4 resembles our specimens. *Phoenicites borealis* Friedrich specimens from Geiseltal (Rüffle 1976) and the Weisselster Basin (Mai & Walther 1985) differ by having twice-bigger stomata and by their thicker cuticular ledges forming the front cavity.

#### ? *Calamoideae* gen. et sp. indet.

Pl. 3, fig. 6; Pl. 13, figs 6–7a

Material. NMA 2016-1/1497.

Description. Fragment of a very strongly armed leaf or petiole, length 108 mm (incomplete), width 30 mm (incomplete); hook-shaped, very massive spines regularly spaced, attached to the ? rhachis or ? petiole, spines 3–4 mm long and up to 3 mm wide at their base; venation of adjacent tissue parallel with perpendicular anastomoses.

Micromorphology. Non-modified cells  $\pm$  distinctly arranged in rows paralleling the length of the ? leaf, but cells not elongated, 7–15 (average 12)  $\mu\text{m}$  long, rectangular to oblique, anticlines thick, appearing in double lines; stomatal complexes loosely spaced, paratracytic to cyclocytic, oriented mainly paralleling leaf length, guard cells sunken, stomatal aperture narrow, spindle-shaped, with distinct cuticular ledges, stoma length 12–19 (average 15)  $\mu\text{m}$ , aperture length 8–11 (average 9)  $\mu\text{m}$ .

Remarks. This remarkable remain is embedded in artificial resin. It definitely derives

from a palm. This is suggested by the parallel venation in combination with the spines and confirmed by the cuticles, i.e., stomatal complexes. Nevertheless, it is somewhat difficult to interpret which part of the leaf is at hand. The regularly spaced spines are attached to one side of a thick, possibly even woody rachis or petiole, whereby on the other side a fragment of the lamina appears attached.

Armature is quite common among palms, and not restricted to Calamoideae (Dransfield et al. 2008).

### **Arecaceae** gen. et sp. indet.

Pl. 3, fig. 5; Pl. 13, figs 7b–8

2008 Problematicum: cf. Arecaceae gen. indet.; Winterscheid & Gregor, p. 6, pl. 3 fig. 1.

Material. NMA 2016–2/1497.

Description. Probably a leaf, petiole stout, length 37 cm, incomplete, width 8 cm, ? lamina consisting of fine, flexible filiform segments, segments up to about 23 cm long, of uncertain arrangement.

Micromorphology. Cells arranged in rows, not clearly traceable, stomata scattered, arranged parallel to cell rows, 36–41  $\mu\text{m}$  long, stomatal complexes probably paratracytic.

Remarks. This specimen is characterised by the peculiar structure of its lamina. The cuticle points towards affinity to Arecaceae. The stomata are distinctly larger than in *Phoenixites* sp. and even larger than in *P. borealis* (Rüffle 1976, Mai & Walther 1985). This specimen was published by Winterscheid and Gregor (2008) erroneously under coll. no. 2006-181/1497.

### Proteales

#### Platanaceae T. Lestib.

#### **Platanus** L.

#### **Platanus neptuni** (Ettingshausen) Bůžek, Holý et Kvaček

Pl. 4, figs 1–10; Pl. 14, figs 1–6

1967 *Platanus neptuni* (Ettingshausen 1866) comb. nov.; Bůžek et al., p. 203, pls 1–4.

2004a *Platanus neptuni* (Ettingshausen) Bůžek, Holý et Kvaček; Kvaček, p. 10, pl. 8, figs 1–13.

Material. SMNS P 1952/ 3, 4, 5, 9, 14, 16, 19, 24 A, 25, 26, 32+97 (part and counterpart),

37, 42, 59, 81+84, 82, 86, cf. 128, 130, 133, 137, 151, 153, 160, 178+179 (part and counterpart), 180, 181, 195, 201, 202, 212, 216, 218, 219, 220, 221, 230, 236, 239, 241, 253, 257, 263, 266, 272, 277, 297, 304, 308, 309, 341, 346, 352, 355, 363, 387, 398, 401, 424, 429, 433, 434, 435, 436, 438, 439, 440, 443+448 (part and counterpart), 462, 464, 465, 467, 469, 474; SMNS P 1953/20, 23, 24A–32, 34, 36–42, 44–46, 67, 78, 83, 96, 98, 120. SMNK 7480, 7598 left, 7664, 7669, 7688, 7727, 7812, 7891. NMA 2006-117/1497, 2006-120/1497, 2006-128, 129/1497, 2006-148/1497, 2006-151/1497, 2006-153/1497, 2006-155/2006, 2006-158/1497, 2006-161/1497.

Description. Simple petiolate leaves, texture coriaceous, lamina oblong, narrow elliptic, mostly symmetric but sometimes also somewhat asymmetric, variable in size,  $l \times w = 29$  (38)–160 (180)  $\times$  15–73 mm,  $l/w$  ratio = 2–4.4; petiole up to 15 mm long, basally widened; base angle acute to obtuse, base straight or somewhat concave to convex, sometimes cuneate to decurrent, apex angle acute, apex straight to acuminate, leaf margin mostly entire near base of the lamina, then simple serrate, sometimes generally almost entire; teeth mainly small with long basal and very short apical sides, apex mainly rounded, sometimes even hook-shaped, densely or widely spaced but at rather regular distances within single leaves, some leaves rather coarsely serrate; midvein mostly straight, secondaries brochidodromous, rather widely spaced, intersecondaries present; further venation details available only from specimen NMA 2006-128/1497: secondaries arching with apically adjacent secondary; marginally, further smaller-scale arches are formed by veinlets originating from secondaries, free veinlets end up in tooth apices of the margin; tertiaries and fourth-order venation random reticulate.

Micromorphology. Adaxial and abaxial cuticle thick, mostly well preserved; anticlines of non-modified epidermal cells slender, mostly distinct, undulated, undulation U-shaped, wide, giving the appearance of puzzle-like indenting, or small and narrow, non-modified epidermal cells 30–70 (average 37–56)  $\mu\text{m}$  adaxially and 22–67 (average 34–47)  $\mu\text{m}$  abaxially across, trichome bases mainly two- to four-celled, single-celled mainly upon veins, periphery strongly thickened, adaxially rare to almost absent, abaxially scattered or more abundant,

inner diameter 12–25  $\mu\text{m}$ , attached peltate trichomes rare, 46–73  $\mu\text{m}$  in diameter, only exceptionally cellular partitioning visible, cuticle surface striate to wrinkled, parallel upon veins and near leaf margin, sometimes present also in non-venous areas, striation stronger and running radially around trichome bases; abaxial cuticle: stomatal complexes anomocytic, irregularly and widely spaced, stomata elliptic,  $l \times w = 27\text{--}45$  (average 32–40)  $\times$  22–38 (average 27–34)  $\mu\text{m}$ ,  $l/w$  ratio = 0.9–1.4 (average 1.1–1.2), epidermal wall of guard cells thickened, ledges thickened, forming an elliptic to broad spindle-shaped outer front cavity, 14–36 (average 18–31)  $\mu\text{m}$  long, aperture  $a \pm$  faint slit.

Remarks. This is by far the most common fossil species at Rauenberg, accounting for about one sixth of all plant remains (>100). Most leaves are symmetric and no compound specimen was recovered. Therefore, we are dealing with leaves of *P. neptuni* rather than with *P. fraxinifolia*-type leaflets. While most specimens can be determined based on gross morphology, some are more ambiguous; some such specimens in the museum's collection were found determined as, for example, *Carya* (P 1952/32+97, part and counterpart, pl. 4, fig. 1). Based on the cuticles, the assignment to *Platanus neptuni* is unambiguous. Although foliage is abundant, no fruiting heads of *Platanus* were detected.

#### Buxales

? Buxaceae Dumort.

#### ? *Buxus* L.

? *Buxus egeriana* Kvaček, Bůžek et Holý

Pl. 6, fig. 19

Material. NMA 2006-168/1497.

Description. Coriaceous, entire-margined leaf, petiole fragmentary, 1 mm long, laminar shape narrow elliptic to oblong,  $l \times w = 27$  (28)  $\times$  8 mm,  $l/w$  ratio = 3.5, base angle acute, base straight, apex ? emarginate, midvein stout, straight, secondaries very densely spaced, probably brochidodromous, single secondaries forking, further venation not discernable, margin strongly thickened, probably by a fimbrial vein.

Micromorphology. Cuticle poorly preserved, anticlines of non-modified cells straight, forming vaguely traceable polygonal cell outlines, stomatal complexes ? anomocytic, roundish with broad spindle-shaped aperture (one well visible, others masked by organic material).

Remarks. This leaf was transferred to artificial resin. The organic material is preserved only fragmentarily but the secondary venation is discernable on the resin surface. The assignment remains somewhat ambiguous because the ramification of the venation characteristic of *Buxus* is not preserved and due to poor cuticle preservation.

Certification of this record would extend the stratigraphic range of *Buxus egeriana*, which was known hitherto from the earliest Miocene (Linz, Austria, Kovar 1982, Cypris Formation, Kvaček et al. 1982).

#### Fagales

Fagaceae Dumort.

#### *Eotrigonobalanus* Walther & Kvaček

##### *Eotrigonobalanus furcinervis*

(Rossmässler) Walther & Kvaček forma

*haselbachensis* (Kvaček & Walther) Kvaček & Walther in Walther

Pl. 6, fig. 14; Pl. 14, fig. 7

1989a *Dryophyllum furcinerve* (Rossmässler) Schmalhausen forma *haselbachensis* forma nova; Kvaček & Walther, p. 220, figs 2 d, 3 a, c.

1989b *Eotrigonobalanus furcinervis* (Rossmässler) Walther & Kvaček forma *haselbachensis* (Kvaček & Walther) comb. nov.; Kvaček & Walther, p. 584, figs 7–10, pls 34–36, pl. 39, figs 2–4, pls 44–46.

2004a *Eotrigonobalanus furcinervis* (Rossmässler) Walther & Kvaček ssp. *haselbachensis* (Kvaček & Walther) Kvaček & Walther in Walther; Kvaček, p. 13, pl. 10, figs 10, 11, 17.

Non 2008 *Eotrigonobalanus furcinervis* (Rossmässler) Walther & Kvaček 1989; Winterscheid & Gregor, pl. 1 fig. 4.

Material. SMNS P 1953/60.

Description. Single petiolate leaf, lamina oblong, slightly obovate,  $l \times w = 85$  (95–100)  $\times$  22 mm,  $l/w$  ratio about 4.4, base angle acute, base cuneate running into the thick petiole, petiole length 5 mm, incomplete, margin entire, midvein straight, stout, secondaries

slender, arising at about 45° and rather regular distances, gently curved, presumably brochidodromous.

**Micromorphology.** Adaxial cuticle not preserved; abaxial cuticle delicate, only above veins anticlines rather well discernable, straight, stomatal complexes in groups, densely spaced, ? cyclocytic, shape roundish, stomata  $l \times w = 19\text{--}25$  (average 22)  $\times$   $20\text{--}23$  (average 22)  $\mu\text{m}$ ,  $l/w$  ratio = 0.9–1.2 (average 1), cuticle above guard cells thin, stomatal ledges indistinct, front cavity short elliptic to roundish, trichome bases scattered, 6–11 (9 average)  $\mu\text{m}$  in diameter.

**Remarks.** Remarkably, this is the only leaf representing the Fagaceae in Rauenberg. Although the cuticle is not very well preserved, its systematic affinity is clear due to the combination of gross morphological and cuticular features. This mainly entire-margined subspecies largely devoid of trichome bases of stellate trichomes is rather common in the late Eocene and early Oligocene. Due to the cuneate leaf base, cf. *Trigonobalanopsis* sp. (Mallison 2002, pl. 10 fig. 1) from the Alzey Formation in the Mainz Basin may represent a leaf of *Eotriginobalanus* rather than of *Trigonobalanopsis*.

#### Betulaceae Gray

##### *Betula* L.

##### *Betula dryadum* Brongniart

Pl. 6, fig. 1

1828 *Betula dryadum* Brongniart, p. 49, pl. 3, fig. 5.

**Material.** SMNK 7711.

**Description.** Two-winged fruit, nutlet narrow obovate, 3.2 mm long, 1 mm wide at widest part, style remnant incomplete, wings skin-like, fruit width including wings about 4.5 mm.

**Remarks.** Fruits of this type are usually assigned to *Betula dryadum*. Often they are found associated with *Betula* bracts as in Armissan (Upper Oligocene, France; Brongniart 1828) or Seifhennersdorf (Lower Oligocene, Germany; Mai 1963). From Rauenberg, however, no bracts have been detected so far, although they are woody and therefore predestined for fossilisation.

#### Betulaceae Gray vel Ulmaceae Mirbel

##### **Betulaceae vel Ulmaceae**

gen. et sp. indet.

Pl. 6, fig. 20; Pl. 14, fig. 8

**Material.** SMNS P 1952/437.

**Description.** Petiolate, membranaceous leaf, petiole slender, 4 mm long, incomplete; lamina asymmetric, ovate,  $l \times w = 56$  (? 62–65)  $\times$  20 mm,  $l/w$  ratio about 3.1–3.3, base angle obtuse, base rounded, apex angle acute, apex shape incomplete, probably straight; margin sharply and densely serrate, probably double serrate; midvein slender, straight, secondaries delicate, somewhat bent, spacing of secondaries 3–5 mm.

**Micromorphology.** Cuticle delicate, anticlines slender, straight to somewhat bent, cell outlines polygonal, 17–22  $\mu\text{m}$  across, ? stomata indicated as more strongly cutinised, broad oval spots, ? anomocytic.

**Remarks.** Gross morphologically, this leaf is reminiscent of Betulaceae and, due to the asymmetric shape, affinity to Ulmaceae cannot be excluded. It remains open whether the scattered thickened regions on the cuticle are interpreted correctly as stomata. From Flörsheim a single leaf ascribed to *Ostrya atlantidis* Unger (Kvaček 2004a) differs by having marginal serration which is distinctly double serrate, with first-order teeth much longer than the second-order ones.

#### Myricaceae Rich. ex Kunth

##### *Comptonia* L. Hérít.

##### *Comptonia difformis* (Sternberg) Berry

Pl. 6, figs 6, 7

1821 *Asplenium difforme*, Sternberg, p. 29, 33, pl. 24 fig. 1.

1825 *Aspleniopteris difformis* Sternberg, p. 21, pl. 24, fig. 1.

1906 *Comptonia difforme* (Sternb.); Berry, 495.

2004a *Comptonia schrankii* (Sternberg) Berry; Kvaček, p. 12, pl. 9, fig. 13.

**Material.** SMNS P 1952/166, SMNS P 1953/118. NMA 2006-146/1497.

**Description.** Pinnate leaves, SMNS P 1952/166 35 mm long (about 2/3 to 3/4 of

complete length preserved), 3.5 mm wide, SMNS P 1953/118 57 mm long, ? half of complete length, 8 mm wide, pinnae tightly spaced, basal side convex, apical side straight to gently concave, attached with full width to midvein, pinnae widest in the middle part of the leaf, tapering towards base and apex; in specimen SMNS P 1953/118, pinnae and especially their margin slightly curled; venation of pinnae not visible.

Remarks. Specimen SMNS P 1952/166 better matches *Comptonia schrankii* (Sternberg) Berry but the other one (SMNS P 1953/118) more closely resembles *C. difformis* (Sternberg) Berry. Kvaček (2004a) supposes that both species reflect ecotypes of a single species rather than discrete species; this is supported by the co-occurrence of the two types in Rauenberg.

### *Myrica* L.

#### *Myrica* cf. *lignitum* (Unger) Saporta sensu Ettingshausen & Standfest

Pl. 4, fig. 11; Pl. 14, fig. 9

1847 *Quercus lignitum* Ung.; Unger, p. 113, pl. 31, figs 5–7.

2004a *Myrica lignitum* (Unger) Saporta; Kvaček, p. 11, pl. 9, figs 11, 12, 16, 17.

Material. SMNS P 1952/361.

Description. Moderately coriaceous leaf, shape somewhat obovate,  $l \times w = 60$  (? 65)  $\times 16$  mm,  $l/w$  ratio about 4.1, base cuneate, petiole not preserved, apex incomplete, ? acuminate, margin entire in the lower part of the lamina, then simple serrate, teeth distinctly developed, hook-shaped, basal side convex, apical side concave, sinus rounded, apex blunt to acute; midvein almost straight, secondaries only exceptionally and faintly traceable, curved upwards eucamptodromous or brochidodromous.

Micromorphology. Cuticle delicate, adaxially and abaxially anticlines straight to curved, distinct, non-modified cells 29–40 (average 35)  $\mu\text{m}$  across adaxially, 19–26 (average 23)  $\mu\text{m}$  abaxially; trichome bases extremely rare, roundish, bicellular, joint anticline of base cells weakly but margin strongly cutinised, inner diameter 10–12  $\mu\text{m}$ , a single peltate trichome observed, 76  $\mu\text{m}$  across; abaxial cuticle: stomatal complexes anomocytic, stomata

roundish, weakly cutinised, aperture broad roundish, acute at poles,  $l \times w = 20\text{--}25$  (average 23)  $\times 20\text{--}23$  (? 27) (average 21)  $\mu\text{m}$ , aperture length 9–12 (average 10)  $\mu\text{m}$ .

Remarks. The wide variability of *Myrica lignitum* leaves is well known not only from the type locality of Parschlug, Austria (Miocene; Kovar-Eder et al. 2004), but also from the marine deposits of the surroundings of Linz, Austria, earliest Miocene (Kovar 1982). The here-described specimen is the only one from Rauenberg that meets *M. lignitum* gross morphologically. Due to the scarcity of peltate trichomes as well as the thinly cutinised anticline separating the base cells of the trichome bases, the assignment remains a bit ambiguous.

Recently, Winterscheid and Kvaček (2014) figured a specimen as *M. lignitum* from Orsberg near Bonn, discussing its gross morphological similarity to *M. joannis* (Ettingshausen) emend. Kovar-Eder. The acute teeth starting already near the leaf base support the assignment to *M. joannis* instead of *M. lignitum*.

#### *Myrica longifolia* Unger

Pl. 4, figs 18–20; Pl. 15, figs 1, 2

1850 *Myrica longifolia*, Unger, p. 159, Taf. 27 Fig. 2, Taf. 28 Fig. 1.

2004a *Myrica longifolia* Unger; Kvaček, p. 11, pl. 9, figs 5–8, 14, 15.

2008 *Myrica lignitum* (Unger 1847) Saporta 1865; Winterscheid & Gregor, pl. 1, fig. 3.

Material. SMNS P 1952/50, 186, 334+335 (part and counterpart); NMA 2006-105/1497, 2006-106/1497.

Description. Narrow linear leaves,  $l \times w = 85\text{--}92$  (? 84–100)  $\times 6\text{--}9$  mm,  $l/w$  ratio = ? 9–16, symmetric, base decurrent, petiole not clearly delimited from base, at least 20 mm long, straight; apex in all specimens incomplete, margin simple serrate, wavy due to its rather widely spaced, small and acute teeth, or almost entire; midrib straight to gently bent.

Micromorphology. Cuticles of both sides thin, abaxially even more delicate than adaxially, preserved in tiny fragments; anticlines of non-modified epidermal cells straight to somewhat bent, abaxially more slender than adaxially, non-modified cells 18–36  $\mu\text{m}$  across,

usually four-celled, rarely two- or three-celled prominent trichome bases, inner diameter (i.e., without margin) 13–24  $\mu\text{m}$ ,  $\pm$  distinctly surrounded by a ring of well-cutinised, thick-walled small cells (sometimes even the cells in the wider surrounding area of a trichome base appear more strongly cutinised); stomata only exceptionally preserved and vaguely discernable, anomocytic nearly roundish, 20–22  $\mu\text{m}$  long ( $n = 2$ ), aperture a short, narrow oval.

**Remarks.** Specimen SMNS P 1952/50 was found determined erroneously as *Sideroxylon*. The successfully prepared tiny cuticle fragments mostly yield a single trichome base and the immediately surrounding area. Judging from these fragments and the cell pattern reflected on them, the area surrounding the trichome base is more strongly cutinised than the remaining cuticle. Diagnostically relevant cuticular features rarely have been described (Mai & Walther 1978, Kvaček 2004a). In the material from Haselbach (Mai & Walther 1978), the trichome bases are two-celled. In Flörsheim, Kvaček (2004a) notes two- to mainly four-celled trichome bases, which matches well with the here-described material in which four- and three-celled bases are more common than two-celled ones. *Myrica lignitum* (Unger) Saporta differs by having clearly two-celled trichome bases. In the Eocene to early Oligocene, *M. longifolia* was widespread from Central Europe to the Tethys and Mediterranean region, including Geiseltal, Häring, Socka, and Armissan, and is often interpreted as indicative of drier climatic conditions (Rüffle 1976).

***Myrica obliquifolia* Kovar-Eder sp. nov.**

Pl. 4, figs 12–17; Pl. 15, figs 3–9

? 2004a *Myrica* cf. *joannis* Ettingshausen 1858 emend. Kovar-Eder 1996; Kvaček, p. 11, pl. 9 figs 9, 10, 18, 19.

**Holotype** designated here. SMNS P 1952/85.

**Paratypes** designated here. SMNS P 1952/162, 232, 238, 255; SMNS P 1953/99.

**Further material.** SMNS P 1952/63+99 (part and counterpart), 204, 386. NMA 2006-142/1497.

**Derivatio nominis.** Referring to the somewhat asymmetric leaf blade.

**Locus typicus.** Rauenberg, Baden-Württemberg, Germany.

**Stratum typicum.** Bodenheim Formation, Hochberg Member, “Fischschiefer”, NP 23, early Oligocene.

**Diagnosis.** Ovate, oblong to elliptic leaves, lamina somewhat asymmetric, margin entire near base, towards apex simple serrate with widely spaced, minute teeth; two-celled trichome bases narrow oval to 8-shaped, joint anticline of base cells very delicate.

**Description.** Leaves ovate, oblong to elliptic, typically somewhat asymmetric, texture thin to medium thick,  $l \times w = 62$  (? 65)–110 (? 120)  $\times$  10–25 mm,  $l/w$  ratio = 4.1– about 7, base angle acute, base straight, cuneate, petiole straight, up to 18 mm long (SMNS P 1952/85), apex long attenuate, apex angle acute, margin basally entire, then minutely simple serrate, teeth widely spaced, density higher apically, teeth narrow, apex acute, sinus acute or rounded; midvein straight or somewhat bent, secondaries craspedodromous or semicraspedodromous (SMNS P 1952/63+99), arising at about 60° angle (SMNS P 1952/85).

**Micromorphology.** Adaxial and abaxial cuticle delicate, anticlines of non-modified cells straight to somewhat curved, non-modified epidermal cells adaxially 18–36 (average 24–25)  $\mu\text{m}$ , abaxially 16–45 (average 24–28)  $\mu\text{m}$  across, two-celled trichome bases rare, oval to 8-shaped, margin strongly cutinised, inner diameter 14–19  $\mu\text{m}$ , joint wall of base cells very delicate, peltate trichomes rarely attached, 75–105  $\mu\text{m}$  in diameter ( $n = 3$ ), margin minimally undulate; abaxial cuticle: stomatal complexes anomocytic, stomata elliptic,  $l \times w$  20–26  $\times$  17–27  $\mu\text{m}$ , aperture elliptic to roundish, 6–8  $\mu\text{m}$  long, poles acute.

**Remarks.** Specimens SMNS P 1952/85, 162, 232, and 255 are the most complete ones. Except for specimen SMNS P 1952/162, which has been transferred to artificial resin, cuticle details are available.

The micromorphology (stomata and peltate trichomes attached to two-celled bases) is suitable for generic identification. These leaves differ from the hitherto known fossil species of *Myrica* by their somewhat asymmetric leaf shape combined with minute and widely spaced teeth. The anticline separating the two

base cells is remarkably delicate, unlike that of, for example, *Myrica lignitum* or *M. undulatifolia* (Knobloch et Kvaček 1976).

*Myrica* cf. *joannis* from Flörsheim (Kvaček 2004a) differs from *M. joannis* Ettingshausen 1858 emend. Kovar-Eder 1996 (Kovar-Eder 1996) by having more abundant and bigger teeth. Moreover, *M. joannis* bears variably straight to undulate anticlines of the non-modified epidermal cells both adaxially and abaxially. In contrast, *M. obliquifolia* shows straight to curved anticlines. It cannot be ruled out, however, that we are dealing here with sun leaves and that the more delicate shade leaves with possibly more undulate anticlines are not preserved in Rauenberg. In this context, note that *Myrica* cf. *joannis* from Flörsheim shows undulate anticlines. Peltate trichomes appear to be rare in both *M. joannis* and *M. obliquifolia*.

An asymmetric base is described for *Myrica hakeaefolia* (Unger) Saporta sensu Engelhardt from Markvartice (Bůžek et al. 1976). These specimens are very fragmentary, the cuticle is not available, and the authors hesitate about the generic affinity.

#### Juglandaceae A. Rich ex Kunth

##### *Carya* Nutt.

##### *Carya fragiliformis*

(Sternberg) Kvaček & Walther

Pl. 6, fig. 22

1825 *Phyllites fragiliformis*, Sternberg, p. 42, pl. 50, fig. 1.

2004a *Carya* sp.; Kvaček, p. 10, pl. 9 fig. 1.

2007 *Carya fragiliformis* (Sternberg) Kvaček & Walther comb. nov.; Walther & Kvaček, p. 110, pl. 11, figs 1–3, pl. 23, figs 8–10.

Material. SMNS P 1952/58.

Description. Single, fragmentary, probably sessile leaflet, texture thin, laminar shape asymmetric, ?oblong to minimally obovate,  $l \times w = 70$  (?100)  $\times$  30 (?35) mm,  $l/w$  ratio about 2.8, base asymmetric, base angle wide acute, base weakly convex, apex not preserved; margin sharply serrate, teeth with acute sinus and apex, basal and apical sides variable, near base straight, convex or concave, and in higher parts of the lamina flexuous to retroflexuous; midvein straight, secondaries densely

spaced, craspedodromous to semicraspedodromous, arising at wide angles of about 80° near the base, higher up angle of origin decreasing, secondaries smoothly bent, subparallel towards each other, sending abaxially further veinlets into the teeth below, terminating in marginal teeth, tertiaries percurrent, course almost straight to somewhat sinuous, angle obtuse.

Remarks. This remains a faint leaf impression with well-preserved venation. It is one of the rare leaf records of temperate deciduous taxa from Rauenberg. The differentiation of *Carya fragiliformis* and *C. serrifolia* is still open (Walther & Kvaček 2007).

##### *Carya quadrangula* (Kirchheimer) Leroy

Pl. 6, fig. 21

2004a *Carya quadrangula* (Kirchheimer) Leroy; Kvaček, p. 11, pl. 9, fig. 2.

Material. SMNS P 1952/159, SMNS P 1953/102.

Description. Somewhat flattened endocarps, elliptic-ovoid in shape,  $l \times w = 36 \times 25$  mm, apex conical-acuminate, base rounded to weakly truncate, surface smooth; specimen SMNS P 1952/159 with two narrow, long lacunae and the separating septum.

Remarks. The two specimens are not only very similar in shape and size to each other but are also strikingly similar to the specimen described from Flörsheim (Kvaček 2004a). Whether *Carya ventricosa* (Schlotheim) Schimper and *C. cf. rostrata* (Schlotheim) Schimper reported from the Alzey Formation (Mallison 2002) are conspecific with the here-described specimens remains open.

##### *Engelhardia* Lesch. Ex Blume

##### *Engelhardia orsbergensis* (Wessel & Weber) Jähnichen, Mai & Walther

Pl. 6, figs 15–17

1855 *Banksia orsbergensis* Wessel & Weber, p. 146, pl. 25, figs 9a–d.

1977 *Engelhardia orsbergensis* (Wess. & Web.) Jähnichen, Mai & Walther comb. nov., p. 326–341.

Material. SMNS P 2228/1. SMNK 7499, 7609+7610 (part and counterpart). NMA 2006-108/1497.

**Description.** Leaflets, laminar shape oblong,  $l \times w = 38\text{--}70 \times 7\text{--}12$  mm, base convex to shortly cuneate, somewhat asymmetric, no petiole, apex angle acute, apex straight, margin simple serrate, teeth distant, tiny, acuminate, midvein straight to gently bent, secondaries and ?intersecondaries arising at  $>45^\circ$  angles and 1–3 mm distances (NMA 2006-108/1497).

**Remarks.** Though no cuticle is available, these are unambiguous records of *Engelhardia orsbergensis* leaflets. The assignment is based on the asymmetric base and the absence of a petiolule, which makes it probable that we are dealing with leaflets that were directly attached to the rhachis. The leaf base variability is well within that of *E. orsbergensis*, as has been demonstrated by Jähnichen et al. (1977) in their comprehensive study of *Engelhardia* from the Palaeogene and Neogene of Europe. Some more leaf fragments may be assigned to either *Engelhardia* or *Myrica*.

***Engelhardia macroptera***

(Brongniart) Unger

Pl. 6, fig. 18

1828 *Carpinus macroptera* Brongniart, p. 48, pl. 3 fig. 6.

1866 *Engelhardia macroptera* (Brongniart) Unger, p. 52, pl. 16, figs 9–11.

**Material.** SMNS P 1952/107, 154+155 (part and counterpart), 206.

**Description.** Incompletely preserved trilobate involucre, lobes entire-margined, narrow, apex rounded, medial lobe 22–33 mm long, lateral one 18 mm long (specimen SMNS P 1952/154), medial lobe somewhat obovate, 6 mm wide in its widest part, width of lateral lobes up to 4 mm, at the base of the involucre only the position of the nutlets is visible; venation (SMNS P 1952/154): medial lobe with three veins running parallel to the lobe length, central vein stronger than lateral ones, further venation reticulate, lateral lobes also with at least two main veins and reticulate further venation.

**Remarks.** Though rare and mainly fragmentarily preserved, these involucre add evidence for the presence of *Engelhardia* in this assemblage. This is remarkable because neither a leaf nor a fruit have been reported from the flora of Flörsheim (Kvaček 2004a).

? Rosales

? Rhamnaceae Juss.

? *Berchemia* Necker ex de Candolle

? *Berchemia altorhenana*

Kovar-Eder sp. nov.

Pl. 5, fig. 5; Pl. 16, figs 7–9

**Holotype** designated here. SMNS P 1953/92.

**Stratum typicum.** Bodenheim Formation, Hochberg Member, “Fischschiefer”, NP 23, early Oligocene.

**Locus typicus.** Rauenberg, Baden-Württemberg, Germany.

**Derivatio nominis.** Referring to the geographical position of the fossil site in the Upper Rhine Graben.

**Stratum typicum.** Bodenheim Formation, Hochberg Member, “Fischschiefer”, NP 23, early Oligocene.

**Diagnosis.** Petiolate leaf, small, elliptic-oblong, base convex, apex rounded, entire-margined to faintly crenate, secondary veins delicate, numerous, regularly spaced; anticlines deeply undulate, undulation rounded to zig-zag, stomatal complexes probably anomocytic, stomata narrow oval, marginally overlapped by a cuticular ledge, front cavity narrow elliptic to narrow spindle-shaped with distinct ledges, stoma orientation probably subparallel, trichome bases with well-staining foot cell, surrounding cells radially arranged.

**Description.** Leaf petiolate, petiole very slender, 6 mm long; almost complete, slightly bent near petiole base; lamina moderately coriaceous,  $l \times w = 25 \times 12$  mm,  $l/w$  ratio = 2.1, shape elliptic-oblong, base convex, base angle obtuse, apex rounded, uppermost apex not preserved, apex angle obtuse, margin entire to faintly crenate; midvein straight, ribbed, secondaries slender, hardly tapering towards leaf margin, densely spaced, about 2–3 mm apart, vein spacing and angle rather regular, veins running strongly parallel to each other, slightly diverging towards the margin, further details not available.

**Micromorphology.** Adaxial and abaxial cuticle delicate, anticlines of non-modified cells slender, smooth, deeply undulate, undulation rounded to zig-zag, non-modified cells 24–38 (average 35)  $\mu\text{m}$  across, simple trichome bases scattered on both surfaces, abaxially more abundant, with foot cell surrounded by radially arranged cells, trichome foot cell 9–14  $\mu\text{m}$  across, well staining; abaxial cuticle: type of stomatal complexes probably anomocytic, stomata narrow oval, marginally slightly overlapped by surrounding cuticle forming a cuticular ledge, stoma  $l \times w = 17\text{--}25$  (average 21)  $\times 10\text{--}21$  (average 15)  $\mu\text{m}$ , front cavity narrow elliptic to narrow spindle-shaped with distinct ledges, 10–17  $\mu\text{m}$  long, stomata orientation probably partly subparallel.

**Remarks.** The dense and parallel spacing of the secondaries, which hardly taper along their course, are reminiscent of Rhamnaceae (*Berchemia*). *Berchemia multinervis* (A. Braun) Heer, known from the Miocene (Bůžek 1971), differs by its bigger leaf size. *Berchemia* has also been described from the Miocene of Kreuzau (Ferguson 1971), including small leaves such as our specimen. *Camptodromites* sp. Kvaček & Teodoridis (2011), originally described by Ettingshausen (1868) as *Berchemia multinervis* from Kučlín, resembles the here-described specimen by its dense secondary venation, but its leaves are sessile. Unfortunately, SMNS P 1953/92 does not provide any information about the tertiary venation, which is characteristic in *Berchemia*, and the records mentioned in this context do not give information on cuticle structure.

Cuticles of 15 southeast Asian species of *Berchemia* have been studied for comparison (Appendix 1). There is no match of the fossil with a single modern species, but the general cuticle characteristics may point towards affinity to *Berchemia*. *B. affinis* Hassk. is similar regarding the zig-zag course of the anticlines and the trichome bases (with a dark-staining centre and girdling cells, pl. 23, fig. 9). The stoma shape of our fossil with somewhat overlapping surrounding cuticle resembles *B. lineata* (L.) DC, for example, and to a lesser extent also *B. kulingensis* Schneider, *B. philippinensis* Vid., and *B. racemosa* S. & Z., whose stomata are deeply sunken among strongly papillae-like domed non-modified cells (pl. 23, figs 7, 8). Regarding stoma orientation, *B. floribunda*

(Wall.) Brongn., *B. lineata*, *B. longeracemosa* Okuyama, and *B. sinica* Schneid. show subparallel stoma orientation resembling *B. altorhenana*. The abaxial cuticle surface of the latter taxa is, in contrast to our fossil, distinctly granulate or granulate-rugulate in *B. lineata*. The stomata of the studied modern species are smaller than in *B. altorhenana*, accounting for some ambiguity of the generic assignment.

? Fabales

? Fabaceae Lindl.

? *Leguminocarpon* Goeppert

? *Leguminocarpon* sp.

Pl. 6, fig. 5

**Material.** NMA 2006-173/1497.

**Description.** Two shortly petiolate pods in opposite position attached to a fragmentarily preserved petiole; pod shape elliptic, one capsule rather complete,  $l \times w$  about  $20 \times 6$  mm, base acute, apex probably shortly acute or somewhat rounded.

**Remarks.** The systematic affinity of these pods remains ambiguous.

Oxidales

Elaeocarpaceae Juss.

*Sloanea* L.

*Sloanea artocarpites*

(Ettingshausen) Kvaček et Hably

Pl. 5, fig. 4

1869 *Quercus artocarpites*, Ettingshausen, p. 63, pl. 55, figs 19, 19a.

1976 *Dicotylophyllum sparsidentatum* sp. n.; Bůžek et al., p. 105, pl. X, figs 1–7, pl. XX figs 5, 6, pl. XXI, figs 1–6, text-fig. 8.

2001 *Sloanea artocarpites* (Ettingshausen) Kvaček et Hably comb. nov.; Kvaček et al., p. 117, pl. 4 figs 8, 9, pl. 6 fig. 8.

2004a *Sloanea artocarpites* (Ettingshausen) Kvaček & Hably; Kvaček, p. 15, pl. 11, figs 6–9, 13–15.

**Material.** SMNS P 1952/61.

**Description.** Middle part of a delicate leaf, base and apex lacking, shape elliptic or ovate, somewhat asymmetric,  $l \times w = ?70 \times 54$  mm,

margin wavy to crenate and minutely serrate, teeth narrow, single, rather widely spaced, apex and sinus acute; midvein slender, straight, secondaries craspedodromous to weakly brochidodromous, relatively widely spaced (up to 18 mm), originating alternately to suboppositely, gently bent, sending abmedial side veinlets towards the margin; no further morphological details or cuticle preserved.

**Remarks.** Based on the serration of the leaf margin and the acute teeth, this leaf resembles *Sloanea artocarpites* more closely than *S. olmediaefolia* (Kvaček et al. 2001). In Flörsheim, *S. artocarpites* is documented by several specimens (Kvaček 2004a). Further occurrences are Seifhennersdorf (Walther & Kvaček 2007), Holý Kluk Mts. (Radon et al. 2006), possibly also Bechlejovice (Kvaček & Walther, 2004), all dated to the early Oligocene.

### *Sloanea olmediaefolia*

(Unger) Kvaček & Hably

Pl. 5, figs 2, 3; Pl. 16, figs 4–6

- 1850 *Artocarpidium olmediaefolium*, Unger, p. 36, pl. 14, figs 1, 2.  
 2001 *Sloanea elliptica* (Andreánszky) Kvaček & Hably comb. nov.; Kvaček et al., p. 117, pl. 2 figs 1–5, pl. 4 figs 1–5, pl. 6 figs 1–7.  
 2008 *Sloanea olmediaefolia* (Unger) Kvaček et Hably; Hably & Kvaček, p. 140, fig. 1: 1–5.  
 2008 *Eotriginobalanus furcinervis* (Rossmäessler 1840) Walther & Kvaček 1989; Winterscheid & Gregor, p. 5, pl. 1, fig. 4.

**Material.** SMNS P 1952/340. NMA 2006-114/1497.

**Description.** Leaves membranaceous, lamina slightly asymmetric, ovate to elliptic,  $l \times w = 82\text{--}88 \times 32$  (34–35)–40 mm,  $l/w$  ratio = 2–2.6; petiole straight, 11 mm long, basally somewhat widened, abscission mark oblique (NMA 2006-114/1497); base cuneate to slightly concavo-convex, apex acuminate; margin wavy dentate, minutely toothed, teeth more closely spaced near base, more widely spaced apically, minute terminal glands probable on some teeth (NMA 2006-114/1497); midvein straight to slightly bent, ?7–8 pairs of secondaries arising alternately to suboppositely, widely spaced, 8–15 mm (NMA 2006-114/1497), running slightly curved across the lamina, ending in tooth apices, craspedodromous, sending off abmedial branches that also end in marginal teeth; tertiaries forked percurrent with

a tendency towards reticulate near the leaf margin, fourth-order veins randomly reticulate (NMA 2006-114/1497); lowermost pair of secondaries arising nearly oppositely at leaf base, ascending steeply near the margin (SMNS P 1952/340).

**Micromorphology.** Adaxial cuticle thick, anticlines distinctly undulate, forming puzzle-like cells 17–28 (average 23)  $\mu\text{m}$  across, glabrous; abaxial cuticle more delicate, anticlines of non-modified cells, undulate, anticlines weakly cutinised, with shorter amplitude and wave length than adaxially, 12–27 (average 17)  $\mu\text{m}$  across (NMA 2006-114/1497), stomatal complexes anomo- to weakly cyclocytic, subsidiary cells somewhat more strongly cutinised (more intensively staining) than the other cells (SMNS P 1952/340), stomata roundish, 11–16 (average 13)  $\times$  10–15 (average 12)  $\mu\text{m}$  (SMNS P 1952/340) and 9–12 (average 10)  $\times$  8–10 (average 9)  $\mu\text{m}$  (NMA 2006-114/1497), aperture elliptic to roundish, 3–5 (average 4)  $\mu\text{m}$  (in both specimens) long, simple trichome bases only above veins, rare.

**Remarks.** Leaf NMA 2006-114/1497 is among the best preserved of all the investigated material. It is not only complete but shows venation details and minute dentation. Its cuticle preservation is less favourable, probably because it was transferred to artificial resin. Although the leaf margin of specimen SMNS P 1952/340 is not preserved, the leaf shape and secondaries are already reminiscent of *Sloanea*, which is confirmed by the well-preserved cuticle. Kvaček (2004a) stressed the differences in the undulation of the anticlines abaxially and the type of stomatal complexes between *Sloanea elliptica* (now *S. olmediaefolia*) and *S. artocarpites*. Accordingly, the here-described leaves match *S. olmediaefolia* better due to the undulated anticlines and the stomatal complexes, which are cyclocytic, though weakly. The cyclocytic type is indicated by more intensively staining subsidiaries in specimen SMNS P 1952/340. The leaf shape and size variability of *S. olmediaefolia* from the Tard Clay between Óbuda (Budapest) and Eger-Kiseged is considerable (Hably & Erdei 2015), and our specimens are closer in size to those from Eger-Kiseged. *S. olmediaefolia* was known previously only from the early Oligocene of the Paratethys Province (Hungary and Slovenia) (Kvaček et al. 2001). Our record extends

its geographical range during the early Oligocene considerably westwards and northwards and is a further substantiation of the floristic relationship between the early Oligocene flora of the Budapest region and that of the western coastal regions of Palaeo-Europe.

Malpighiales

Salicaceae Mirb.

*Populus* L.

*Populus germanica* (Menzel) Walther

Pl. 5, fig. 6

- 1926 *Menispermites germanicus* Menzel, p. 32, figs 1–3.  
 1978 *Populus germanica* (Menzel) comb. nov.; Walther, p. 90, pl. 3, fig. 16, pl. 8, figs 1–9, pl. 9, figs 1, 2, pl. 36, figs 1–8, pl. 37, figs 1–5.  
 2004a *Populus germanica* (Menzel) Walther; Kvaček, p. 15, pl. 11, figs 10–12.

Material. SMNK 7568, ? 7725. NMA 2006-107/1497.

**Description.** Membranaceous leaves, petiole lacking,  $l \times w = ?55\text{--}70 \times 60\text{--}70$  mm (SMNK 7568, NMA 2006-107/1497) and  $9 \times 12$  mm (SMNK 7725), shape suborbicular, base rounded (SMNK 7568) and ?concavo-convex (SMNK 7725), apex ?rounded to obtuse, ?acuminate in the uppermost part (SMNK 7725), margin wavy (SMNK 7568); midrib straight, secondaries craspedodromous, basal secondaries arising directly at base, position of further secondaries subopposite, almost straight (SMNK 7568) or slightly bent (SMNK 7725), single secondaries forking or sending abmedial veinlets, terminating in glandular marginal teeth or lobe sinus; tertiaries percurrent, fourth-order venation reticulate, fimbrial vein  $\pm$  distinct along leaf margin (SMNK 7568).

**Remarks.** Specimens SMNK 7568 and NMA 2006-107/1497 are embedded in synthetic resin. This enables the leaf venation to be traced in transmitted light and reveals the existence of a fimbrial vein (SMNK 7568). Because the very small lamina, the assignment of specimen SMNK 7725 may be ambiguous. Kvaček (2004a) pointed to the similarity of *Populus germanica* and *P. leuce* (Rossmässler) Unger from the Staré Sedlo Formation (Knobloch et al. 1996), stating that the two species may be conspecific but that the cuticle structures

are unknown for *P. leuce*. The relatively small size of the lamina accounts for the systematic assignment to *P. germanica*.

Malvales

Malvaceae Juss.

*Craigia* W.W. SM. et W.E. Evans

*Craigia bronniei*

(Unger) Kvaček, Bůžek et Manchester

Pl. 6, fig. 2

- 1845 *Ulmus bronniei* Unger, p. 79 pro parte, pl. 25, figs 2–4.  
 1991 *Craigia bronniei* (Unger); Kvaček, Bůžek et Manchester, p. 552.

Material. SMNK 7748 (part and counterpart).

**Description.** Flattened, detached, oval valves of a fruit capsule, 12 mm long with peripheral, incompletely preserved wing, diameter 27 (?30) mm, partly preserved as compression and partly as imprint, central suture well visible, wing poorly preserved, only main veins discernable, spreading radially, sometimes dichotomising towards margin.

**Remarks.** In this poorly preserved, rather large specimen, seeds are not demarcated and it remains open whether it was sterile. *Craigia* is best known from the North Bohemian brown coal region, where it is preserved in the form of different organs: fruits, foliage, flowers, and flower buds (Kvaček 2004c). This is the only record of *Craigia* in the flora from Rauenberg.

Saxifragales

Hamamelidaceae R. Br. In C. Abel

*Distylium* Siebold et Zucc.

*Distylium metzleri* Kovar-Eder sp. nov.

Pl. 6, fig. 23; Pl. 16, figs 1–3

Holotype designated here. SMNS P 1952/43.

Stratum typicum. Bodenheim Formation, Hochberg Member, “Fischschiefer”, NP 23, early Oligocene.

Locus typicus. Rauenberg, Baden-Württemberg, Germany.

**Derivatio nominis.** In honour of Rudolf Metzler, one of the major collectors of the flora from Rauenberg.

**Diagnosis.** Slender, smooth concentric epicuticular wrinkles developed upon guard cells and subsidiary cells, wrinkles thicker, distinct and parallel upon veins, trichome bases scattered above veins, cuticular wrinkles near trichome bases  $\pm$  radially oriented.

**Description.** Apical two thirds of a simple, asymmetric leaf, texture thin, laminar shape elliptic or ovate,  $l \times w = 51$  (? 65)  $\times$  22 mm, apex almost straight to somewhat acuminate, apex angle acute, leaf margin entire in the central part of the leaf but sparsely and minutely denticulate near apex; secondaries faintly visible, brochidodromous, widely spaced (distance between two adjacent secondaries 13 mm), veins diverging from the secondaries towards the leaf margin, forming further loops, a single intersecondary and few tertiaries visible, the latter percurrent.

**Micromorphology.** Cuticles of both sides very thick and well preserved; anticlines of non-modified epidermal cells thick, undulate, slightly knobby; undulation shallower adaxially than abaxially, non-modified cells almost equal in size on both sides, adaxially 26–31 (average 32)  $\mu\text{m}$ , abaxially 23–40 (average 31)  $\mu\text{m}$ ; abaxial cuticle: stomatal complexes brachyparacytic, somewhat asymmetric due to subsidiary cells that are partly unequal in size; pair of guard cells elliptic oblong, 18–26 (average 21)  $\times$  19–23 (average 22)  $\mu\text{m}$ ,  $l/w$  ratio = 0.8–1.3 (average 0.9), outer front cavity narrow oval, almost reaching the poles, formed by distinct cuticular ledges, epidermal wall of guard cell not very distinct, poles somewhat thickened; upon guard and subsidiary cells, slender concentric cuticular wrinkles developed; single, big and prominent, thickly cutinised trichome bases above veins, one to two rings of small cells surrounding the trichome base centre, inner diameter about 20  $\mu\text{m}$ , diameter including girdling cells about 70  $\mu\text{m}$ , epicuticular wrinkles distinct, thick and radially arranged around trichome bases but running parallel above veins.

**Remarks.** This is one of the rare leaf findings in this flora showing secondary veins and tertiaries. Unfortunately, the basal part of the lamina is not preserved. The combination of

features – asymmetric lamina, brachyparacytic stomata, and the characteristic trichome bases – indicate affinity to the Hamamelidaceae. *Distylium fergusonii* differs by its entire margin also near the leaf apex, by the abaxial cuticle which is less strongly cutinised than the adaxial one, and by the greater abundance of trichome bases. The epicuticular structure is clearly highly variable, from almost absent (Mai & Walther 1978, there as *D. cf. fergusonii*; Ferguson 1971) to well developed in the material from Wackersdorf (Knobloch & Kvaček 1976) and Oberdorf (Kovar-Eder & al. 2001). *D. fergusonii* plexus from the Kristina mine, Hrádek, bears thick cuticles on both sides, and the strong wrinkles abaxially obscure the anticlines of the non-modified cells (Holý et al. 2012). Leaves of *D. heinickei* (Mai & Walther 1991) bear tiny marginal teeth, as does the here-described specimen. Studies of the type and original material revealed that the cuticle is very delicate and the epicuticular structure is less strongly developed, and in *cf. Distylium sp.* (Walther 1999) the cuticle is smooth. No delicate concentric crinkles have been reported on the guard and subsidiary cells in *D. fergusonii* or in *D. heinickei*.

Since leaves of *Distylium* are rather rare in the fossil record and usually not abundant at single sites, it is difficult to judge fossil species variability. Especially for *D. fergusonii* the variability of the described records is broad, raising doubts about whether they all are conspecific.

? Santalales

? Loranthaceae Juss.

? *Viscophyllum* Knoll

? *Viscophyllum hendriksiae* Kovar-Eder  
sp. nov.

Pl. 7, figs 1–5; Pl. 23, figs 1–6

Holotype designated here. SMNS P 1953/70.

Paratypes. SMNS P 1952/11, 57, 158; SMNS P 1953/71, 77. NMA 2006-134/1497.

Stratum typicum. Bodenheim Formation, Hochberg Member, “Fischschiefer”, NP 23, early Oligocene.

**Locus typicus.** Rauenberg, Baden-Württemberg, Germany.

**Derivatio nominis.** In honour of Janine Hendriks, technician at NMA, for her assistance in my study of the collection there.

**Description.** Long-petiolate, leathery, entire-margined leaves, petiole up to at least 25 mm long and up to 3 mm thick, broader near petiole base, often bent; lamina elliptic to broad elliptic,  $l \times w = 35$  (? 38)–56  $\times$  15–31 mm,  $l/w$  ratio = 1.6–3.4, base cuneate, gradually tapering into the petiole, apex angle acute, shape (almost) straight, utmost apex blunt; midvein straight, visibly continuing into the petiole, midvein thick and pronounced in specimen SMNS P 1952/11 but slender and hardly visible in other specimens, secondaries very delicate, widely spaced, steeply ascending and arching about 1–2 mm in front of the margin (brochidodromous) (NMA 2006-134/1497), further details unclear.

**Micromorphology.** Cuticle thick, glabrous, anticlines mainly straight, thick but often not well traceable, hypostomatic; adaxial cuticle: non-modified epidermal cells polygonal, very large, up to 114  $\mu\text{m}$  across, cell surface subdivided into smaller fields indicating ?hypodermis; abaxial cuticle: non-modified epidermal cells  $\pm$  distinctly arranged in rows, subquadrangular to pentagonal, with central thickened papilla, cells about 22–43  $\mu\text{m}$  across (SMNS P 1952/11), that is, much smaller than stomata, or non-modified cells polygonal as in non-stomata bearing condition, stomata  $\pm$  completely surrounded by a thick cuticular fold, thus type of stomatal complexes ambiguous, stomata arranged parallelly (SMNS P 1952/11) or randomly (SMNS P 1952/158), oval to almost roundish,  $l \times w = 43$ –83  $\times$  33–57  $\mu\text{m}$ , epidermal wall of guard cell indistinct, cuticular ledges very thick, forming an elliptic to broad spindle-shaped, very prominent, 34–56  $\mu\text{m}$  long front cavity, aperture short, narrow oval to spindle-shaped, parallel epicuticular striation present, on guard cells concentric; SEM study did not yield further details.

**Remarks.** The texture of specimens SMNS P 1952/11 and 57 is extremely leathery; in SMNS P 1952/158 and SMNS P 1953/71 it is less leathery but still thick. In all these specimens the carbonised leaf material is fragmented into tiny splinters, while the lamina

of SMNS P 1953/70 and 77 appears skin-like, unfragmented and brownish. In all specimens the cuticle is thick but mainly present in small fragments. The cuticular features leave no doubt that these specimens are conspecific. In particular, this concerns stoma shape and size as well as the peculiar cell pattern in non-stoma bearing condition (large polygonal cells with a network of smaller meshes indicative of a ? hypodermis). In SMNS P 1952/158 the stomata are randomly distributed, while in the other specimens the stoma orientation appears rather parallel. It remains open whether the differences in stoma orientation are related to the problem that cuticle samples were obtained mainly from near the leaf margin close to the leaf base to avoid coverage by varnish.

These leaves probably are assignable to the fossil genus *Viscophyllum* Knoll. *V. weylandii* (Walther) Walther (Mai & Walther 1985), described from the Upper Eocene of the Weiselster Basin, is similar in leaf shape and in the steeply ascending secondaries; it differs by its smaller leaf size, smaller stomata (which are wider than long) and the type of stomatal complexes with clearly visible subsidiaries.

## Cornales

### Hydrangeaceae Dumortier

#### *Hydrangea* L.

##### *Hydrangea microcalyx* Sieber 1881

Pl. 6, fig. 4

1881 *Hydrangea microcalyx*, Sieber, p. 16 pro parte: figs 26, 27, 31.

2014 *Hydrangea microcalyx* Sieber 1880; Winter-scheid & Kvaček.

**Material.** SMNS P 1952/145.

**Description.** Tetramerous, petaloid calyx, 17 mm in diameter, single calyx leaves elliptic to roundish in shape, tapering towards base, point of attachment to axis narrow, apex obtuse or somewhat emarginate, entire-margined, every leaf shows a midvein running straight into the apex, especially the basal secondaries arise at narrow angles, ascending steeply, eventually forking across the lamina, further details not available.

**Remarks.** Only a single specimen is available from the abundant material which is

surprisingly well preserved. Its four leaves are unfused, closely spaced and touching each other. The specimens from Kučlín (Sieber 1881, Kvaček & Teodoridis 2011) differ in that the leaves are obovate and not as closely spaced as in the specimen from Rauenberg. The latter more closely resembles the specimen from Seifhennersdorf figured by Mai (1963: pl. 10, fig. 9) and the specimen from Hammerunterwiesenthal (Walther 1998: Abb. 2 fig. 20). The specimens from Seifhennersdorf (Walther & Kvaček 2007: pl. 13 figs 7, 8) are incomplete and thus not well comparable. This large variability, however, is within the natural variability of *Hydrangea* species Mai (1963).

*H. microcalyx* is an accessory element in the volcanic floras of Bohemia and Saxony from the late Eocene to Oligocene. The revision of the flora from Orsberg near Bonn also includes *H. microcalyx* (Winterscheid & Kvaček 2014). This is the first record from the Oligocene coastal floras of the Rhein Graben.

The east Asian *H. paniculata* Sieb. et Zucc., *H. petiolaris* Sieb. et Zucc., and *H. quercifolia* Bartr. from North America are regarded as the most similar relatives (Mai 1963).

#### Ericales

? Pentaphragmaceae Engl. in Engl. & Prantl

? *Ternstroemites* Berry emend. Hickey

#### ? *Ternstroemites maritiae*

Kovar-Eder sp. nov.

Pl. 5, fig. 7; Pl. 17, figs 1–3

Holotype designated here. SMNS P 1952/342.

Stratum typicum. Bodenheim Formation, Hochberg Member, “Fischschiefer”, NP 23, early Oligocene.

Locus typicus. Rauenberg, Baden-Württemberg, Germany.

Derivatio nominis. Dedicated to Marit Kamenz, technician at the SMNS, who patiently made numerous cuticle preparations for this study.

Description. Apical fragment of a coriaceous, probably entire-margined leaf,  $l \times w = 35$  (?70)  $\times$  22 (?24) mm, laminar shape unclear, apex angle acute, apex shape nearly straight.

Micromorphology. Adaxial and abaxial cuticle thick, glabrous; anticlines of non-modified epidermal cells densely undulate but not very pronounced, cells 32–49 (average 42)  $\mu\text{m}$  across; abaxial cuticle: anticlines of non-modified epidermal cells even less distinct than adaxially, undulate but faintly traceable only (cell size not measureable), type of stomatal complexes unclear, stoma elliptic, stomata surrounded by a thick cuticular wrinkle, guard cells less strongly cutinised, occasionally with concentric striae, cuticular ledges strongly thickened, forming a narrow oval outer front cavity, stoma  $l \times w = 32$ –45 (average 38)  $\times$  26–35 (average 30)  $\mu\text{m}$ ,  $l/w$  ratio = 1.1–1.5 (average 1.3), aperture length 24–35 (average 29)  $\mu\text{m}$ , cuticle surface with scattered, almost parallel wrinkles.

Remarks. Laminar shape and size remain ambiguous due to the fragmentary preservation of this leaf. The cuticle suggests a possible relationship to the Pentaphragmaceae. Stoma shape and size, the concentric wrinkles around the stomata, and the occasionally occurring,  $\pm$  parallel wrinkles covering the abaxial surface may point towards affinity to *Gordonia*. The very dense undulation of the anticlines on the adaxial cuticle raises uncertainty, however.

#### Symplocaceae Desf.

#### *Symplocos* Jacq.

#### *Symplocos deichmuelleri* (Kvaček & Walther) comb. nov.

Pl. 5, figs 8–10; Pl. 17, figs 4–6

1998 *Dicotylophyllum deichmuelleri* Kvaček & Walther, p. 14 pl. 6, figs 7–12.

2004a *Symplocos volkeri* Kvaček sp. n., Senckenberg Lethaea, 84, p. 17, pl. 14, figs 2, 3, 13–15.

2007 *Dicotylophyllum deichmuelleri* Kvaček & Walther; Walther & Kvaček, p. 127, pl. 18, figs 16, 17, pl. 24, figs 12, 13.

2008 *Eotrigonobalanus furcinervis* (Rossmassler 1840) Walther & Kvaček 1989; Winterscheid & Gregor, pl. 1 fig. 4.

2014 *Symplocos volkeri* Kvaček 2004; Winterscheid & Kvaček, p. 30, pl. 5 figs 7, 8, pl. 12 fig. 1.

2014 *Dicotylophyllum deichmuelleri* Kvaček et Walther; Kvaček et al., p. 42, figs 7G–J, 8L.

Material. SMNS P 1952/62, 65, 79+98 (part and counterpart), SMNS P 1953/43.

**Description.** Petiolate leaves, texture medium thick,  $l \times w = 40\text{--}55$  (? 58)  $\times$  17–33 mm,  $l/w$  ratio = 1.8–2.8, laminar shape broad elliptic to slightly obovate, petiole 4–9 (? complete) mm long, bent or straight, basally widened (SMNS P 1952/65); base angle acute to almost 90°, base rather straight to concave near the very base and then somewhat convex, apex angle acute to obtuse, apex straight to somewhat acuminate; margin almost entire near the base with only single teeth, simple serrate with more densely spaced teeth towards apex, teeth  $\pm$  tiny, basal and apical sides almost straight, sinus rounded or acute, apex rounded or (bluntly) acute and glanduliferous; midvein straight, secondaries markedly more delicate than midvein (SMNS P 1952/62), arising at about 40–50° angle from midvein, angles of adjacent veins variable, near their origin running almost parallel to midvein before turning outwards, tertiaries percurrent, course slightly convex to sinuous, higher-order veins forming a dense network.

**Micromorphology.** Adaxial cuticle delicate, abaxial cuticle thick, both sides glabrous; adaxial cuticle with faint anticlines, straight to bent, non-modified cells 18–33  $\mu\text{m}$  across; abaxial cuticle: non-modified cells distinct, smaller than stomata, 13–26 (average 17–18)  $\mu\text{m}$  across, surface of non-modified cells papilla-like thickened, anticlines straight to curved, stomatal complexes brachyparacytic, stomata not sunken, narrow oval, only faintly if at all delimited from narrow subsidiaries, stoma  $l \times w = 19\text{--}29$  (average 21–24)  $\times$  14–18  $\mu\text{m}$ , aperture narrow oval, 6–9  $\mu\text{m}$  long, cuticular ledges distinct, almost reaching the poles, slender polar I-pieces sometimes present, faint concentric striation on stomata (SMNS P 1952/62).

**Remarks.** Specimens SMNS P 1952/62 and SMNS P 1953/43 show secondary veins near the base. In the latter the tertiary and higher-order venation is also well visible, while its cuticle is less well preserved than in the other remains. The cuticle is best preserved in specimen SMNS P 1952/65. In SMNS P 1952/62 the marginal teeth in the apical part of the lamina are bigger and the apical glands on the teeth are distinctive. In the other specimens the glanduliferous teeth are easy to miss.

The features of the abaxial cuticle of *Symplocos volkeri* and *Dicotylophyllum deichmuelleri*

are very similar and Kvaček et al. (2014) already suggested *Symplocos* as the probable genus for the leaves assigned to *D. deichmuelleri*.

Comparing the leaves from Flörsheim and Rott (Kvaček 2004a, Winterscheid & Kvaček 2014), *S. deichmuelleri* shows considerable variability in leaf shape and secondary venation but consistency regarding the cuticular structures. The figure of Kvaček (2004a: pl. 14, fig. 14) suggests papilla-like thickenings on the surface of non-modified cells, as in the material from Rauenberg. This was confirmed by comparative studies of the original cuticular slides from Flörsheim. Although smaller than the leaves from Flörsheim, those from Rauenberg more closely resemble the record from Flörsheim than the specimens from Rott. No glands have been reported from the tooth apices of specimens from Flörsheim or Rott. More material is therefore necessary to decide whether we are dealing with a single species.

## Gentianales

### Apocynaceae Juss.

#### *Trachelospermum* Kvaček

#### *Trachelospermum kelleri*

Kovar-Eder sp. nov.

Pl. 6, figs 24, 25; Pl. 18, figs 3–5

**Holotype.** NMA 2006-121/1497.

**Paratype.** SMNS P 1953/101.

**Stratum typicum.** Bodenheim Formation, Hochberg Member, “Fischschiefer”, NP 23, early Oligocene.

**Locus typicus.** Rauenberg, Baden-Württemberg, Germany.

**Derivatio nominis.** In honour of the private collector Manfred Keller, who donated his collection to the Naturmuseum Augsburg.

**Diagnosis.** Long-petiolate, narrow oblong to slightly obovate, entire-margined leaves, base acute to cuneate, apex acute, venation delicate; cuticles delicate, small mesophyllous secretory bodies very dense, remains of ? guard cells and secretory material masking the cuticular features of the stomata.

**Description.** Long-petiolate, entire-margined, coriaceous leaves; petiole 11–14 mm long (almost complete), straight to slightly bent, basally slightly widened and with longitudinal folds (NMA 2006-121/1497); base cuneate, base angle acute, shape straight; apex angle acute, shape straight (NMA 2006-121/1497); lamina narrow, oblong or slightly obovate,  $l \times w = 75$  (? 80–85)  $\times$  15 mm,  $l/w$  ratio = ? 5.3–5.7 (SMNS P 1953/101),  $l \times w = 38 \times 11$  mm,  $l/w$  ratio = 3.4 (NMA 2006-121/1497); venation delicate, midvein straight, secondaries slender, connecting at different distances from margin, intersecondaries present; secondaries, intersecondaries and tertiaries forming irregular vein network with meshes of different sizes and shapes.

**Micromorphology.** Cuticle of both sides delicate, non-modified cells not discernable, cuticular features of stomata characteristically masked by intensively staining remains of the ? guard cells and secretory material, stomatal complexes ? anomocytic, stomata (broadly) oval, somewhat oblique in shape, recessed at poles,  $l \times w = 24\text{--}30 \times 19\text{--}27$   $\mu\text{m}$  (SMNS P 1953/101,  $n = 4$ ) and  $21\text{--}28$  (average 24)  $\times$   $15\text{--}18$  (average 17)  $\mu\text{m}$  (NMA 2006-121/1497), length of stomatal aperture 17  $\mu\text{m}$  ( $n = 1$ ); densely packed with mesophyllous, differently sized secretory bodies up to 12  $\mu\text{m}$  in diameter (NMA 2006-121/1497).

**Remarks.** These remains are to be assigned to the genus *Trachelospermum* as defined by Kvaček (2004a). They differ in leaf shape and venation from *T. steiningeri*. Micromorphological differences are the absence of anticlines of non-modified cells, the presence of ? guard cell remains and secretory material masking the stomatal cuticular features, the shape of the stomatal aperture, and probably also the type of stomatal complex.

Apocynaceae gen. (Kvaček 2004a) is similar in leaf shape, the presence of dense secretory bodies in the mesophyll, and stoma shape. It differs from the here-described specimens by the short petiole and dense spacing of the secondaries. Although Apocynaceae gen. shows similarity to *Dicotylophyllum* sp. 11 from Kundratice (Kvaček & Walther 1998) in leaf shape and venation, the cuticles of the latter species differ by the type of the stomatal complex, aperture shape, idiocuticular striation and the lack of mesophyllous secretory bodies.

### *Trachelospermum steiningeri* Kvaček

Pl. 6, figs 26, 27; Pl. 17, figs 7–9; Pl. 18, figs 1, 2

2004a *Trachelospermum steiningeri*, Kvaček, p. 18, pl. 15, figs 1–8, 11–15.

**Material.** SMNS P 1952/101, 366.

**Description.** One complete leaf (SMNS P 1952/101) and one fragment lacking base, apex and margin (SMNS P 1952/366), moderately coriaceous; SMNS P 1952/101: laminar shape wide elliptic,  $l \times w = 38 \times 25$  mm,  $l/w$  ratio = 1.5, petiole straight, 8 mm long, incomplete; base concave, base angle acute, apex angle obtuse, apex retuse, margin entire, somewhat undulate; midvein straight, distinctly tapering apically, secondaries slender, arising at angles of about 50–60°, angles decreasing apically, distance between secondaries up to 5 mm (in the central part of the lamina); course slightly diverging between each other and somewhat concave near the margin, intersecondaries probably present.

**Micromorphology.** SMNS P 1952/101: cuticle of both sides delicate, glabrous, anticlines only faint, smoothly curved to somewhat wavy, non-modified epidermal cells 18–34 (average 25)  $\mu\text{m}$  across adaxially and 17–20  $\mu\text{m}$  ( $n = 3$ ) across abaxially, small secretory bodies very dense, diameter 10–15  $\mu\text{m}$ ; abaxial cuticle: type of stomatal complexes questionable, stomata broad oval to roundish,  $l \times w = 14\text{--}18 \times 12\text{--}19$   $\mu\text{m}$ ,  $l/w$  ratio = 0.9–1.2 ( $n = 5$ ), epidermal wall of guard cells hardly developed, guard cells hardly staining, stomatal ledges slender, slightly thickened, forming short, broad spindle-shaped front cavity with acute poles, length of front cavity 9–10  $\mu\text{m}$ , aperture a faint slit.

SMNS P 1952/366: adaxial and abaxial cuticle well preserved, glabrous, smooth, anticlines of non-modified cells straight to moderately bent, slender, non-modified epidermal cells polygonal, on both sides very similar in size, 19–34 (average 25)  $\mu\text{m}$  across; abaxial cuticle: stomatal complexes cyclocytic, subsidiary cells similar in size and shape to non-modified cells but less strongly cutinised, stomata elliptic,  $l \times w = (22) 25\text{--}31$  (average 25)  $\times$   $19\text{--}23$  (average 21)  $\mu\text{m}$ ,  $l/w$  ratio = 1.2–1.6 (average 1.3), epidermal wall of guard cells faintly visible only, ledges slender, not strongly cutinised, forming an elliptic front cavity, length

(7) 11–17 (average 14)  $\mu\text{m}$ , aperture slit-like, poles I-like, slightly thickened; small, secretory bodies present.

Remarks. The gross morphology of specimen SMNS P 1952/101 points to affinity to *Trachelospermum*, but specimen SMNS P 1952/366 is too fragmentary for any assignment based on gross morphology. In both specimens the shape of the stomata and front cavity as well as the small secretory bodies, which are dense in specimen SMNS P 1952/101, support this assignment. The cyclocytic stoma complex type is evident in SMNS P 1952/366 only. Kvaček (2004a) described it as anomocytic to incompletely cyclocytic for the specimens from Flörsheim. The different interpretations are not contradictory but probably result from the fact that the cuticles from Flörsheim were unstained and that the thinly cutinised subsidiaries are probably more difficult to discern there. In specimen SMNS P 1952/101 the stomata are smaller and more roundish than in specimen SMNS P 1952/366 (therefore described separately), but in both the stoma length is within the variability provided by Kvaček (2004a). However, no giant stomata have been observed in the here-studied material. At first glance the adaxial cuticle of SMNS P 1952/366 gives the impression of domed non-modified cells, but this interpretation reflects the dense remains of small secretory bodies.

*Trachelospermum steiningeri* is known so far only from Flörsheim and Rauenberg, and the number of available specimens is still very limited, leaving intraspecific variability poorly understood.

Kvaček (2004a) compares *T. steiningeri* to *T. asiaticum* (Sieb. & Zucc.) Nakai, an evergreen woody liana of upland forests and brushwood, and to further *Trachelospermum* species in SE Asia.

## Lamiales

### Oleaceae Hoffmanns & Link

#### *Oleinites* Cookson emend. Sachse

#### *Oleinites altorhenana* Kovar-Eder sp. nov.

Pl. 5, figs 17, 18; Pl. 18, figs 6–9

Holotype designated here. SMNS P 1952/191.

Paratypes. SMNS P 1952/388; SMNS P 1953/62.

Stratum typicum. Bodenheimer Formation, Hochberg Member, “Fischschiefer”, NP 23, early Oligocene.

Locus typicus. Rauenberg, Baden-Württemberg, Germany.

Derivatio nominis. Derived from the geographical position of the fossil site in the Upper Rhine Graben.

Diagnosis. Broad elliptic to ovate, medium-sized leaves, non-modified cells abaxially remarkably small, stomata densely spaced, subcircular, epidermal and poral wall of guard cells indistinct, prominent simple bases of probably peltate trichomes with rim-like thickened margin.

Description. Leaves elliptic to ovate, texture moderately thick,  $l \times w$  up to  $115 \times 43$  mm,  $l/w$  ratio = 2.6 (SMNS P 1953/62), margin entire to smoothly undulate, base angle obtuse, shape somewhat convex, apex angle acute, shape acuminate; midvein slender, straight, secondaries poorly visible, delicate, originating at about  $50^\circ$  angle, vein spacing about 10 mm in the basal half of the lamina, secondaries running almost straight close to the margin (SMNS P 1953/62).

Micromorphology. Adaxial cuticle less robust than abaxial one, unequivocally preserved only in SMNS P 1952/191; both surfaces finely striate along veins; adaxially, anticlines of non-modified epidermal cells curved to somewhat sinuous, 17–27 (average 21)  $\mu\text{m}$  across, while abaxially distinctly smaller, 6–17 (average 12)  $\mu\text{m}$  across; in SMNS P 1952/388 anticlines of non-modified cells not traceable; abaxial surface: stomatal complexes anomocytic, stomata more weakly cutinised than the other parts of the abaxial surface, epidermal and poral wall of guard cells indistinct, stomata roundish,  $l \times w = 16\text{--}21$  (average 18)  $\mu\text{m} \times 16\text{--}23$  (average 18)  $\mu\text{m}$ , aperture broad elliptic to roundish, 6–9 (average 8)  $\mu\text{m}$  long; simple trichome bases scattered, inner diameter 5–13  $\mu\text{m}$ , margin collar-like, 4–9  $\mu\text{m}$  thick, surrounding cells  $\pm$  radially arranged, occasionally with faint radial folding, trichome heads disc-shaped or globular about 20–25  $\mu\text{m}$  in diameter (? and bigger).

Remarks. The most complete specimen is SMNS P 1953/62 but the cuticle is best preserved in SMNS P 1952/191, which represents only the apical half of a leaf. The adaxial cuticle either had less preservation potential or else the unclear details of the cell outlines hamper its recognition. Only in specimen SMNS P 1952/191 is the adaxial cuticle unambiguous. The type of trichome base as well as the roundish, weakly cutinised and thus indistinct stomata point to the morphogenus *Oleinites* (Sachse 2001). This new fossil species differs from *Oleinites hallbaueri* (Mai) Sachse by the entire margin of the leaves, and from *O. hallbaueri* and *O. maii* (Bůžek, Holý & Kvaček) Sachse by the small, roundish stomata which are hardly delimited from the non-modified cells with short, elliptic to roundish aperture, and by an adaxial cuticle that is usually difficult to identify. *O. pachyphyllus* (Kvaček 2004a), described from Flörsheim, differs both in gross morphology (elongate, narrower leaf) and in cuticular features (much thicker cuticles, larger non-modified cells and large stomata).

*Oleinites altorhenana* more closely resembles *O. liguricus* from Torre Sterpi, northern Italy, Messinian (Sachse 2001) both macro- and micromorphologically. As in the here-introduced fossil species, the adaxial cuticle of *O. liguricus* is difficult to discern. Apart from the difference in age, *O. liguricus* differs by having somewhat larger stomata.

Among modern genera, similar trichome bases and roundish stomata occur in *Chionanthus* and *Olea* (Sachse 2001).

### ***Oleinites rauenbergensis***

Kovar-Eder sp. nov.

Pl. 5, figs 12–16; Pl. 19, figs 1–6

Holotype designated here. SMNS P 1952/380.

Paratypes. SMNS P 1952/299, 402.

Further material. ? SMNS P 1952/6; ? SMNS P 1953/93 (pl. 5, figs 15, 16).

Stratum typicum. Bodenheim Formation, Hochberg Member, “Fischschiefer”, NP 23, early Oligocene.

Locus typicus. Rauenberg, Baden-Württemberg, Germany.

Derivatio nominis. Referring to the type locality.

Diagnosis. Small, spatulate, entire-margined coriaceous leaves, cuticle very thick, brittle, non-modified epidermal cells very large, anticlines undulate, stomatal complexes subcircular, widely spaced, epidermal wall of guard cells faintly developed but poral wall well developed; simple trichome bases prominent.

Description. Leaves obovate, spatulate, texture coriaceous,  $l \times w = 13\text{--}20$  (?  $25$ )  $\times$   $4\text{--}11$  mm,  $l/w$  ratio =  $2.5\text{--}3.3$ , base cuneate to decurrent with gradual transition into a ? short petiole, apex rounded to somewhat emarginate, margin entire, midvein slender, straight, no further details available.

Micromorphology. Adaxial cuticle very thick, abaxial cuticle somewhat thinner, cuticle of both sides characteristically brittle, breaking into tiny fragments, simple trichome bases scattered, abaxially probably more common than adaxially, with strongly thickened, collar-like margin (up to  $10\ \mu\text{m}$ ), surrounding cells  $\pm$  radially arranged, thickened, sometimes radially elongated, a single small head found attached,  $39\ \mu\text{m}$  in diameter (SMNS P 1952/380); adaxial cuticle: anticlines up to  $3\text{--}4\ \mu\text{m}$  thick, widely and shallow undulate, non-modified cells  $22\text{--}64$  (average  $36\text{--}48$ )  $\mu\text{m}$  across; abaxial cuticle: anticlines of non-modified cells poorly visible, stomatal complexes ?anomocytic, widely spaced, subcircular, epidermal wall of guard cells poorly developed, ledges thickened, forming a broad elliptic front cavity with acute poles, short, slender polar I-pieces sometimes weakly developed, stoma size  $l \times w = 22\text{--}30 \times 20\text{--}26\ \mu\text{m}$  (in all specimens only few stomata available), length of front cavity  $10\text{--}14\ \mu\text{m}$ , double-contoured.

Remarks. The cuticle of this fossil species is preserved mainly in very tiny fragments representing few cells, and only a few stomata were suitable for taking measurements. From the smallest leaf (SMNS P 1952/299,  $l \times w = 13 \times 4$  mm) the adaxial cuticle is available, and the abaxial side probably is represented by a tiny fragment with a single trichome base. Based on the obovate, spatulate lamina along with the thick and brittle cuticle, the undulated course of the anticlines adaxially and the trichome base, this specimen is grouped here. Nonetheless, adaxially the non-modified

epidermal cells are smaller (average 36  $\mu\text{m}$ ). In specimen SMNS P 1952/6 it is unclear whether the trichome bases are one-celled. Specimen SMNS P 1953/93 is similar in gross morphology except for the distinctly thickened leaf margin. From this specimen only the adaxial cuticle is available. The size and pattern of the non-modified cells correspond to those of *Oleinites rauenbergensis*.

These spatulate small leaves are reminiscent of Ericaceae and especially of the recently described *Andromediphyllum ungeri* from Flörsheim (Kvaček 2004a). The cuticle, however, differs by its brittleness, much bigger cells adaxially, the thick abaxial cuticle with smaller stomata lacking distinct striae, as well as the presence of trichome bases of the *Oleinites* type. *Oleinites dieteri* (Kovar-Eder) Kvaček (Kvaček 2004a) from early Miocene lignite deposits of Styria (Kovar-Eder & Meller 2001) is similar in leaf size and shape but differs by the acute to acuminate apex and marginal serration. The cuticle of the latter species is brittle and the cells of the adaxial cuticle are similarly large with undulate anticlines, as in the here-described material. Moreover, the stomata resemble *O. rauenbergensis* in shape and size and peltate trichomes are present. The strong idiocuticular striation, however, distinguishes *O. dieteri* from *O. rauenbergensis*. The Oleaceae affinity of these small spatulate leaves continues to be disputable.

Fam. indet.

***Pungiphyllum*** Frankenhäuser & Wilde

***Pungiphyllum cruciatum***

(Al. Braun) Frankenhäuser & Wilde

Pl. 5, fig. 11

1995 *Pungiphyllum cruciatum* (Al. Braun 1851) nov. comb.; Frankenhäuser & Wilde, p. 101.

2004a *Pungiphyllum cruciatum* (Al. Braun) Frankenhäuser & Wilde; Kvaček, p. 19, pl. 16, fig. 11.

Material. NMA 2006-126/1497.

Description. Basal half of lamina, length and width incomplete,  $l \times w = 55 \times 25$  mm, base cuneate, base angle acute, base almost straight, petiole 5 mm long, incomplete, straight, laminar shape not evident, with deep lobation, two lobes preserved, sinus widely rounded, apex

spinose; midvein straight, secondaries craspedodromous, intersecondaries present, adjacent ones looping, secondaries and intersecondaries arising at angles of  $>60^\circ$ , tertiaries and higher-order veins polygonal reticulate, with marginal fimbrial vein.

Remarks. This leaf is preserved as a faint imprint with little carbonized material especially along the veins and leaf margin. The leaf surface is covered by abundant roundish fruiting bodies of fungi.

Gross morphologically, *Pungiphyllum waltheri* from the Eocene plant site Eckfeld differs by the pattern of the tertiary venation where the tertiaries arise from the midvein between the secondaries (Frankenhäuser & Wilde 1995). The here-described specimen closely resembles the specimen from Kundratice figured by Kvaček & Walther (1981: pl. 7 fig. 1), for example, where the tertiaries originate perpendicularly mainly from the secondaries, forming a polygonate network.

The single remain reported from Flörsheim (Kvaček 2004a) represents the apical half of a leaf. Although *P. cruciatum* is a characteristic element of Oligocene and Miocene plant assemblages, it occurs mainly as an accessory element.

***Dicotylophyllum*** incertae sedis

***Dicotylophyllum badense***

Kovar-Eder sp. nov.

Pl. 7, fig. 16; Pl. 19, figs 7–9

Holotype designated here. SMNS P 1952/200.

Stratum typicum. Bodenheim Formation, Hochberg Member, "Fischschiefer", NP 23, early Oligocene.

Type locality. Rauenberg, Baden-Württemberg, Germany.

Derivatio nominis. Rauenberg, the fossil site, is located in Baden, Baden-Württemberg.

Diagnosis. Leaf coriaceous, narrow, entire-margined, cuticles thick, anticlines straight to curved, stomatal complexes cyclocytic, oval to roundish, front cavity formed by distinct cuticular ledges, reaching the poles, polar I-thickenings moderately developed, aperture short oval, simple trichome bases rare.

**Description.** Fragment of the middle part of a narrow leaf lacking base and apex,  $l \times w = ? 40 \times 18$  mm, entire-margined, midvein somewhat bent, texture very coriaceous.

**Micromorphology.** Adaxial and abaxial cuticle thick, anticlines straight to curved, shape and size of non-modified cells on both sides very similar, 15–30  $\mu\text{m}$  (average 23)  $\mu\text{m}$  across; simple, well-cutinised trichome bases abaxially and ? adaxially present but rare; stomatal complexes cyclocytic, subsidiary cells very similar to non-modified epidermal cells but more intensively staining, stomata oval to roundish,  $l \times w = 24\text{--}37$  (average 30)  $\times$  25–34 (average 29)  $\mu\text{m}$ , epidermal wall of guard cells often indistinct, front cavity 5–17 (average 11)  $\mu\text{m}$  long, almost reaching the poles, formed by thick and broad cuticular ledges, aperture short oval, polar I-thickenings  $\pm$  well developed.

**Remarks.** Remarkable is the extremely firm texture causing a peculiar pattern of cracks that is unique among the plant remains of Rauenberg. So far, no putative taxonomic affinity can be suggested for this leaf.

### *Dicotylophyllum oechsleri*

Kovar-Eder sp. nov.

Pl. 7, fig. 17; Pl. 22, figs 1–4

**Holotype** designated here. SMNS P 1952/454.

**Stratum typicum.** Bodenheim Formation, Hochberg Member, “Fischschiefer”, NP 23, early Oligocene.

**Locus typicus.** Rauenberg, Baden-Württemberg, Germany.

**Derivatio nominis.** Dedicated to Harald and Annette Oechsler, who have collected the Rauenberg plant site systematically for many years.

**Diagnosis.** Coriaceous leaf with spiny marginal teeth; adaxial and abaxial cuticle leathery, anticlines undulate, stomatal complexes loosely spaced, anomocytic to indistinctly cyclocytic, subsidiary cells corresponding in shape and size to non-modified cells, stomata elliptic to subcircular, front cavity short elliptic to roundish, prominent trichome bases of probably peltate glandular trichomes scattered.

**Description.** Leaf fragment lacking base and apex, texture coriaceous,  $l \times w = 29$  (? 55–60)  $\times$  18 (19–20) mm, laminar shape probably elliptic, margin coarsely serrate, teeth spiny, sinus rounded, basal and apical sides straight to concave; midvein slender, somewhat bent, secondaries craspedodromous, forking or sending abmedial veinlets into the tooth apices, further venation reticulate but exact details unclear.

**Micromorphology.** Adaxial and abaxial cuticle thick with scattered simple trichome bases, margin collar-like thickened, surrounding cells short, radially arranged, the ? disc-shaped or globular head left a depression and a circular marginal ridge on the cuticle surface; adaxial cuticle: anticlines slender, deeply sinuous, cuticle surface distinctly, coarsely striate, non-modified epidermal cells 29–54 (average 41)  $\mu\text{m}$  across; abaxial cuticle: anticlines thick, sinuous, non-modified epidermal cells 37–54 (average 46)  $\mu\text{m}$  across, stomatal complexes anomocytic to indistinctly cyclocytic, subsidiary cells corresponding in shape and size to non-modified cells, stomata elliptic to subcircular,  $l \times w = 25\text{--}29$  (average 26)  $\times$  18–26 (average 22)  $\mu\text{m}$ , guard cells less strongly cutinised than other cells, ledges well developed forming a broad elliptic to roundish front cavity, 9–13 (average 10)  $\mu\text{m}$  long.

**Remarks.** Gross morphologically this leaf is reminiscent of *Ilex* (Walther & Kvaček 2008) or *Mahonia* (Kvaček & Bůžek 1994). The cuticular features do not confirm an affinity to *Mahonia*. The variability of the epidermal features of *Ilex* is wide (Baas 1975), making comparisons a challenge. Especially the stomata and type of stomatal complexes are diverse (Baas 1975, plate 2). *Ilex aquifolia*, for example, bears a thick adaxial cuticle with undulate anticlines and strong striation (Walther & Kvaček 2008) alike *Dicotylophyllum oechsleri*. In *I. opaca* the trichome bases resemble those encountered on our fossil (Walther & Kvaček 2008, pl. 6 fig. 9). *Ilex* foliage from Kreuzau (Germany, Miocene; Ferguson 1971) bears no resemblance gross morphologically, the adaxial cuticle is devoid of striae, and the stomatal complexes are clearly cyclocytic, but the stomata resemble our fossil in shape and size, as do the non-modified epidermal cells of the abaxial cuticle. Trichome bases also occur but remained unfigured and therefore cannot be compared. *Ilex castelii* Kvaček & Walther

(Kvaček & Walther 1981) differs by, among other characters, the absence of striae adaxially and abaxially by having bigger stomata with a thickened outer margin and broad ledges forming the front cavity. *I. knoblochii* (Walther 1999) described from Kleinsaubernitz (Germany, Upper Oligocene) differs by its smaller undulation both in amplitude and wave length adaxially and abaxially, stomata arranged in groups, the presence of T-shaped polar thickenings, and the lack of trichome bases. Due to all these differences this leaf remains assigned to *Dicotylophyllum* only.

***Dicotylophyllum vesiculaeferens***

Kovar-Eder sp. nov.

Pl. 7, figs 7, 8; Pl. 20, figs 1–5; Pl. 21, figs 1–3

Holotype designated here. SMNS P 1952/310.

Paratype. SMNS P 1952/306.

Further material. ? SMNS P 1952/414.

Stratum typicum. Bodenheim Formation, Hochberg Member, “Fischschiefer”, NP 23, early Oligocene.

Locus typicus. Rauenberg, Baden-Württemberg, Germany.

Derivatio nominis. Referring to the vesicle-like, secretion-bearing structures (idioblasts).

Diagnosis. Narrow, entire-margined leaves, cuticles delicate with pentagonal to hexagonal pocket-like structures, single or, more often, occurring in groups or even adjacent to each other, each with a central plurilet mark, sometimes still bearing vesicle-like secretory bodies.

Description. Leaves coriaceous, laminar shape narrow, oblong to somewhat obovate,  $l \times w = 52$  (? 55)– $64$  (? 75)  $\times$  8–17 mm,  $l/w$  ratio = ?4.4–6.8, entire-margined, margin thickened, base angle acute and narrow acute, base straight, apex angle narrow acute, apex straight or somewhat acuminate.

Micromorphology. Specimen SMNS P1952/310: Adaxial cuticle moderately thick, anticlines mainly slender, straight to finely undulate, partly pitted, non-modified cells 17–25 (average 21)  $\mu$ m across; simple trichome bases scattered, trichome pore surrounded by

somewhat radially elongated and slightly more strongly cutinised cells, single secretory structures (see abaxial cuticle) occur sporadically; abaxial cuticle delicate, anticlines of non-modified epidermal cells almost straight to slightly bent, faintly visible if at all; cells polygonal, 14–24 (average 19)  $\mu$ m across, stomata weakly cutinised, difficult to discern, anomocytic, sometimes with tendency towards cyclocytic, roundish often asymmetric, stoma  $l \times w = 11$ –18 (average 14)  $\times$  12–22 (average 17)  $\mu$ m,  $l/w$  ratio 0.7–0.9 (average 0.8), aperture short, slit-like or narrow oval, no thickened ledges developed, simple trichome bases as on adaxial cuticle, scattered; pentagonal to hexagonal pocket-like structures, 11–17 (14)  $\mu$ m in diameter, occurring in groups or even adjacent to each other, each with central tetralet to hexalet mark, sometimes still bearing vesicle-like secretory bodies; under SEM these structures appear elevated above the external cuticle surface, occasionally cuticle remnants of head still adherent.

Remarks. The most remarkable feature of these leaves is the mainly pentagonal to hexagonal pouches with a central asterix-like tetralet to hexalet mark, balloon-shaped secretory bodies, as well as cuticle remains of the head sometimes still adherent. The cuticle of specimen SMNS P 1952/306 is more poorly preserved and mainly hexagonal pouches are discernable. The material was studied by both light microscopy and SEM, but SEM studies were successful only on the external surface (prior to separating the cuticles). It remains unclear whether the secretory vesicles were secreted only below the cuticle or above it in a gland-like structure or both. These structures may have served to secrete salt or possibly other minerals. Complex salt glands do occur in different genera of the Chenopodiaceae, Tamaricaceae and Plumbaginaceae sensu Watson & Dallwitz (1992 onwards) (Salama et al. 1999).

The plant assemblage from Rauenberg also yields articulate twig fragments with cuticles bearing pouches sometimes still yielding vesicle-like secretory bodies. The pouches are roundish or irregular in shape, however, not distinctly pentagonal to hexagonal. The twigs probably derive from the same plant species as the leaves because these structures are very extraordinary (see *Cladites vesiculaeferens* sp. nov.).

***Dicotylophyllum ziegleri***

Kovar-Eder sp. nov.

Pl. 7, fig. 6; Pl. 21, fig. 9; Pl. 22, figs 5–7

**Holotype** designated here. SMNS P 1953/86.

**Stratum typicum.** Bodenheim Formation, Hochberg Member, “Fischschiefer”, NP 23, early Oligocene.

**Locus typicus.** Rauenberg, Baden-Württemberg, Germany.

**Derivatio nominis.** In honour of the late Prof. Bernhard Ziegler, director of the Stuttgart State Museum of Natural History 1969–1994.

**Diagnosis.** Entire-margined, narrow obovate, shortly petiolate leaf; non-modified cells large, abaxially large cyclocytic to somewhat actinocytic stomatal complexes, stomata narrow oval, ledges thickened, front cavity narrow spindle-shaped, almost reaching the poles, lacking polar T-pieces, aperture slit-like, discus- or bowl-shaped multicellular glands somewhat recessed in cuticle and overlapped by surrounding cells.

**Description.** Shortly petiolate, medium-thick leaf, laminar shape narrow obovate,  $l \times w = 42 \times 11$  mm,  $l/w$  ratio = 3.8, petiole 2 mm long (? incomplete), almost 2 mm wide, basally widened; base cuneate, straight, base angle acute, apex angle acute, in the uppermost part obtuse, apex slightly retuse; midvein straight.

**Micromorphology.** Adaxial and abaxial cuticle well preserved, medium thick, smooth; anticlines slender but distinct, almost straight, non-modified epidermal cells 34–61 (50)  $\mu$ m across adaxially and 26–45 (38)  $\mu$ m across abaxially; abaxial cuticle: stomatal complexes widely spaced, subparallel among each other, cyclocytic to slightly actinocytic, 5–8 subsidiary cells, similar in shape and size to non-modified cells but less intensively staining, guard cells narrow oval,  $l \times w = 36\text{--}50$  (45)  $\times$  23–31 (27)  $\mu$ m,  $l/w$  ratio = 1.2–1.9 (1.7), epidermal wall of guard cell usually weakly cutinised, stomatal ledges strongly thickened, forming a narrow spindle-shaped front cavity, almost reaching the poles, aperture a faint slit; multicellular glands sunken and marginally overlapped by surrounding, marginally strongly thickened cells, diameter of pouches 34–47  $\mu$ m ( $n = 5$ ); SEM study yielded no further details.

**Remarks.** Due to its large non-modified cells and stomatal complexes, along with the presence of epidermal secretory bodies, this leaf is reminiscent of *Illicium*, but cuticular studies of modern *Illicium* (Oh et al. 2003) indicate differences. Modern species were compared based on photographs provided by T. Denk, one of the co-authors of the mentioned paper. The cuticular features are rather consistent across modern species of *Illicium*. The stomatal complexes are brachyparacytic or more rarely (hemi)amphibrachyparacytic showing distinct polar T-pieces (Oh et al. 2003), while they are cyclocytic to actinocytic and lacking polar T-pieces in the here-described specimen. In *Illicium* the etherial oil cells are surrounded by 6–8 radially elongated cells, whereas in our specimen the surrounding cells are not elongated and the glands are sunken in pouches. In *Illicium* the anticlines are mainly undulate and the cuticle shows strong idiocuticular ornamentation, unlike *Dicotylophyllum ziegleri* in which the cuticle is smooth and the anticlines are straight.

*Illicium eocenicum* (Jähnichen 1976), which is to be excluded from *Illicium* according to Oh et al. (2003), differs by the presence of polar T-pieces and the strong idiocuticular pattern from *Dicotylophyllum ziegleri*. *Illicium geiseltalensis* (Jähnichen 1976) – also to be excluded from *Illicium* (Oh et al. 2003) – differs by having smaller stomata with T-pieces, smaller non-modified epidermal cells and secretory cells, and idiocuticular striation (Mai & Walther 1985).

“*Illicium*” *limburgense* Kräusel & Weyland (Walther 1999) from Kleinsaubernitz is similar due to the presence of glands which appear sunken and overlapped by neighbouring cells and rather large stomata (though smaller than in *D. ziegleri*), but differs in leaf shape, petiole length, stoma shape and shape of the front cavity, and in having smaller glands and strong idiocuticular folding. Finally, there is no resemblance to the leaves of species XLIX in Ferguson (1971) that were previously described as *Illicium fliegelii* (Weyland 1934).

***Dicotylophyllum* sp.**

Pl. 7, fig. 18; Pl. 22, figs 8, 9

**Material.** SMNS P 1952/400.

**Description.** Petiolate, small leaf, rather complete, only apical quarter missing; petiole

straight, 7 mm long (? complete), almost 1 mm wide, surface corrugated; lamina elliptic, texture medium thick,  $l \times w = 25$  (? 30)  $\times$  18 mm,  $l/w$  ratio about 1.7, base angle obtuse, base convex; margin entire, thickened, midvein straight, venation suprabaasal acrodromous, basal secondaries arising almost oppositely about 1 mm above base, running at distance of 2–3 mm from the leaf margin, almost parallel to it and hardly tapering into the uppermost quarter of the lamina, no further veins visible.

**Micromorphology.** Cuticles of both sides delicate, membranaceous, preserved in larger fragments, distinction between the two sides difficult due to faint stomata; anticlines indistinct, slender, almost straight, curved to slightly wavy, non-modified cells 18–34 (average 22)  $\mu\text{m}$  across adaxially, 13–22 (average 19  $\mu\text{m}$ ) across abaxially, trichome bases present abaxially and ?adaxially, prominent, girdling cells  $\pm$  distinct, roundish to pie-slice-like in shape,  $\pm$  radially elongated, arranged concentrically around the trichome pore in one complete and sometimes a second incomplete circle, margin of trichome pore thickened, trichome pores 10–14  $\mu\text{m}$  ( $n = 5$ ) in diameter; abaxial cuticle: stomatal complexes only very rarely vaguely discernable, paracytic, broadly butterfly-like due to broad lateral subsidiary cells, stomata ? sunken, 12–13  $\mu\text{m}$  long ( $n = 2$ ), stomatal ledges indistinct, outer front cavity narrow spindle-shaped, almost reaching the poles.

**Remarks.** Gross morphologically, Hamamelidaceae, e.g., *Matudaea* (Mai & Walther 1978), malvalean affinity, e.g., *Byttneriopsis* (Kvaček & Wilde 2010), or Lauraceae may be considered for this entire-margined, three-veined leaf. From the *Daphnogene*-type, this leaf differs by its rather delicate basal secondaries arising almost oppositely and very close to the base, running into the apical third of the lamina, hardly diminishing in width. Paracytic stomatal complexes occur in, for example, Ericaceae, Hamamelidaceae, or Magnoliaceae, while sunken ones may point to Lauraceae affinity. In the here-discussed specimen they are very small and only vaguely discernable if at all. Similar trichome bases do occur among Lauraceae, for example in shade leaves of *Daphnogene* (pl. 9, figs 4, 5). Oil-bearing idioblasts, as encountered in Lauraceae or

Magnoliaceae, have not been observed in this specimen. The systematic position of this leaf therefore remains ambiguous.

### *Cladites* D.H. Scott

#### *Cladites vesiculaeferens*

Kovar-Eder sp. nov.

Pl. 7, figs 9–14, 19; Pl. 20, figs 6–9; Pl. 21, figs 4–8

**Holotype.** SMNS P 1952/416.

**Paratypes.** SMNS P 1952/87, 371.

**Material.** SMNS P 1952/104, 157; SMNS P 1953/105. NMA 2006-154/1497, NMA 2016-4/2179. SMNK 7778.

**Stratum typicum.** Bodenheim Formation, Hochberg Member, “Fischschiefer”, NP 23, early Oligocene.

**Locus typicus.** Rauenberg, Baden-Württemberg, Germany.

**Derivatio nominis.** Referring to the vesicle-like structures embedded in the cuticle.

**Diagnosis.** Telescope-like articulate axes, branched; cuticle: non-modified epidermal cells short,  $\pm$  in parallel rows, with  $\pm$  clustered pouches, cuticle there thinner, sometimes with central plurilet mark, secretory bodies of very different size sometimes still adherent, balloon-shaped, originating as protuberances and embedded in pouches.

**Description.** Fragments of telescope-like articulate axes, branched (SMNS P 1952/87), segment length very variable, 2 mm (SMNS P 1952/87) to 26 mm (SMNS P 1952/371), segment width 2–6 mm.

**Micromorphology.** Cuticle very thick, anticlines strongly cutinised in older parts of branches but thin in apical/distal part; non-modified epidermal cells short,  $\pm$  in parallel rows, pockets developed, cuticle there thinner, pockets  $\pm$  clustered, variable in size, about 20–50  $\mu\text{m}$  in diameter, sometimes with a central trilet to tetralet mark, secretory bodies of very different size, balloon-shaped, sometimes still adherent, originating as protuberances and embedded in pouches; in SEM view secretory bodies appear interconnected (pl. 21, fig 6); external surface of these structures in SEM view roundish to somewhat

angular concavities with  $\pm$  distinct centre and  $\pm$  distinctly developed marginal cuticular rim (pl. 21, figs 7–8).

**Remarks.** These articulate stems, lacking stomata, superficially are reminiscent of rhizomes. The pocket-like structures of the cuticles are similar to those described for *Dicotylophyllum vesiculaeferens*. They differ in being more roundish or only weakly angular, and no complex structures elevated above the cuticle surface have been observed. The cuticle from a more distal part of the axis SMNS P 1952/416 implies that secretional structures developed from the cuticle and were embedded in it (pl. 20 fig. 9). Collection compartments separating the cuticle from the epidermis have been described from Tamaricaceae, Frankeniaceae, and Plumbaginaceae (Salama et al. 1999). The present structures possibly are similar. I suggest that the cross-like mark represents the region where the secretion was transferred to the stem surface. Depending on whether situated on the leaf or the stem, glands may be raised on the cuticle surface or sunken among epidermis cells, for example in Plumbaginaceae (*Limoniastrum axillare*, *L. monopetalum*) (Salama et al. 1999). The fragments of articulate branches and *D. vesiculaeferens* therefore probably derive from the same fossil species, and the complex secretory structures may represent salt glands (see also the section describing *Dicotylophyllum vesiculaeferens*). As for *D. vesiculaeferens*, the systematic affinity of the articulate stems remains open.

A similar remain from Flörsheim has been described as a rhizome (Kvaček 2004a, rhizome B). This specimen was studied for comparison, but it is an impression only, devoid of organic material.

#### Winged fruit or seed incertae sedis

Pl. 6, fig. 3

**Material.** NMA 2006-113/1497.

**Description.** One-winged oval fruit or seed,  $l \times w = 7 \times 4$  mm, wing membraneous,  $l \times w = 17 \times 9$  mm, dorsal line continuing rather straight to seed or fruit body, ventral line curved, no veins visible.

**Remarks.** This remain may be of coniferous origin. Fruits of *Cedrelospermum* are smaller,

and their vein-bearing wings are attached obliquely to the fruit body.

#### Spiny branch

Pl. 7, fig. 15

**Material.** NMA 2006-23/1497.

**Description.** Fragment of axis, 23 mm long and about 2 mm wide, with spiny acute apex, two suboppositely originating branches, one of them complete, 52 mm long, terminating also in attenuate spine, the second branch incomplete.

**Remarks.** The main axis and the branches are clearly acute and attenuate spiny. This remain is similar to Fabaceae but spiny axes also occur in other families, for example in Rosaceae such as *Crataegus* or *Prunus*.

## RESULTS

The plant assemblage of Rauenberg yielded 68 fossil species (Tab. 1). Three different types of marine algae were distinguished, among them representatives of the Phaeophyceae with aerocysts (*Cystoseirites communis*). Most remains, mainly leaves but also seed cones and other fructifications, derive from terrestrial plants.

The taxonomic assignment of the terrestrial plant remains is based both on gross morphology and on cuticular features. Twenty-six families are documented, but nine taxa cannot be assigned to the family level. Fourteen fossil species of angiosperms are described for the first time: *Laurophyllum rauenbergense* (Lauraceae), *Myrica obliquifolia* (Myricaceae), *Distylium metzleri* (Hamamelidaceae), ? *Viscophyllum hendriksiae* (? Loranaceae), ? *Berchemia altorhenana* (? Rhamnaceae), ? *Ternstroemites maritiae* (? Pentaphragmaceae), *Trachelospermum kelleri* (Apocynaceae), *Oleinites altorhenana*, *O. rauenbergensis* (Oleaceae), *Dicotylophyllum badense*, *D. oechsleri*, *D. vesiculaeferens*, *D. ziegleri*, and *Cladites vesiculaeferens*. The diversity of Lauraceae (10) is highest, followed by Pinaceae (8), Arecaceae (4–5), Myricaceae (4), Cupressaceae (3), Taxodiaceae (2), Cupressaceae (1), and Juglandaceae (3). All other families – Schizaeaceae, Zamiaceae, Doliostroboaceae, Platanaceae, ? Buxaceae, Fagaceae, Betulaceae, Betulaceae/Ulmaceae, ? Rhamnaceae, ? Fabaceae, Elaeocarpaceae, Salicaceae, Malvaceae, Hamamelidaceae, ? Loranaceae,

**Table 1.** List of taxa and physiognomy. Abundance categories: I – 1 specimen, II – 2–5 specimens, III – 6–10 specimens, IV – 11–50 specimens, V – < 50 specimens. Laminal sizes in the Rauenberg flora: nanophyll 25–225 mm<sup>2</sup>, microphyll 225–2.025 mm<sup>2</sup>, notophyll 2.025–4.500 mm<sup>2</sup>, mesophyll 4.500–18.225 mm<sup>2</sup> (Webb 1955), calculated  $l \times w \times 2/3$  (see Leaf Architecture Group 1999)

Taxon	Organ type	Abundance	Leaf margin	Texture	Laminal size
<b>Algae</b>					
<i>Cystoseyrites communis</i>		I			
<i>Thallites multifidus</i>		IV			
<i>Laminarites latus</i>		IV			
<b>Ferns</b>					
<i>Lygodium kaulfussii</i>	leaflet	II			
<i>Filicopsida</i> sp.	leaflet	I			
<b>Cycads</b>					
<i>Ceratozamia floersheimensis</i>	leaf	I			
<b>Conifers</b>					
<i>Doliosirobus taxiformis</i> ? <i>taxiformis</i>	leafy twig	I			
<i>Sequoia abietina</i>	leafy twig	I			
<i>Taxodium</i> sp.	leafy twig	II			
<i>Tetraclinis salicornioides</i>	leafy twig	IV			
<i>Pinus (Strobilus)</i> sp. 1	fascicle	I			
<i>Pinus (Strobilus)</i> sp. 2	fascicle	II			
<i>Pinus (Strobilus)</i> sp. 3	fascicle	II			
<i>Pinus (Strobilus)</i> sp. 4	fascicle	I			
<i>Pinus</i> sp. 5	fascicle	II			
<i>Pinus</i> sp. 6	fascicle	I			
<i>Pinus (Pinus)</i> cf. <i>thomasiana</i>	cone	II			
<i>Pinus engelhardtii</i>	cone	I			
<b>Angiosperms</b>					
<i>Actinodaphne pseudogermari</i>	leaf	I	entire	coriaceous	notophyll
<i>Daphnogene cinnamomifolia</i>	leaf	V	entire	coriaceous	nanophyll-notophyll
<i>Laurus abchasicus</i>	leaf	II	entire	moderately coriaceous	microphyll
<i>Laurophyllum kinkelinii</i>		II	entire	moderately coriaceous	microphyll
<i>Laurophyllum</i> cf. <i>kinkelinii</i> var. <i>glabrum</i>	leaf	II	entire	moderately coriaceous	microphyll
<i>Laurophyllum pseudoprinceps</i>	leaf	IV	entire	coriaceous	microphyll
<i>Laurophyllum rauenbergense</i>	leaf	IV	entire	coriaceous	nanophyll, microphyll
<i>Laurophyllum</i> sp. A	leaf	I	entire	coriaceous	microphyll
<i>Laurophyllum</i> sp. B	leaf	I	entire	coriaceous	? microphyll
<i>Laurophyllum</i> sp. C	leaf	I	entire	coriaceous	microphyll
<i>Palmacites lamanonis</i>	leaf	IV			
<i>Sabalites major</i>	leaf	II			
<i>Phoenicites</i> sp.	leaf	II			
? <i>Calamoideae</i> gen. et sp. indet.	leaf/petiole	I			
Arecaceae gen. et sp. indet.	leaf	I			
<i>Platanus neptuni</i>	leaf	V	basally entire, then serrate	coriaceous	micro- to mesophyll
? <i>Buxus egeriana</i>	leaf	I	entire	coriaceous	nanophyll
<i>Eotrigonobalanus furcinervis</i> f. <i>haselbachensis</i>	leaf	I	entire	coriaceous	microphyll
<i>Betula dryadum</i>	winged fruit	I			
Betulaceae vel Ulmaceae gen. et sp. indet.	leaf	I	sharply ? double serrate	membranaceous	microphyll
<i>Comptonia difformis</i>	leaf	II		coriaceous	? nanophyll, microphyll

Table 1. Continued

Taxon	Organ type	Abundance	Leaf margin	Texture	Laminar size
<i>Myrica cf. lignitum</i>	leaf	I	basally entire, then serrate	moderately coriaceous	microphyll
<i>Myrica longifolia</i>	leaf	II	almost entire to serrate	moderately coriaceous	microphyll
<i>Myrica obliquifolia</i>	leaf	III	basally entire, then minutely serrate	delicate to moderately coriaceous	microphyll
<i>Carya fragiliformis</i>	leaf	I	sharply serrate	membrana- ceous	notophyll
<i>Carya quadrangula</i>	fruit	II			
<i>Engelhardia orsbergensis</i>	leaflet	II	serrate	membrana- ceous	nanophyll, microphyll
<i>Engelhardia macroptera</i>	involucrum	II			
? <i>Berchemia altorhenana</i>	leaf	I	entire	moderately coriaceous	nanophyll
? <i>Leguminocarpon</i> sp.	fruit	I			
<i>Sloanea artocarpites</i>	leaf	I	wavy dentate, minutely toothed	membrana- ceous	notophyll
<i>Sloanea olmediaefolia</i>	leaf	II	wavy dentate, minutely toothed	membrana- ceous	microphyll, notophyll
<i>Populus germanica</i>	leaf	II	wavy	membrana- ceous	microphyll
<i>Craigia bronni</i>	fruit	I			
<i>Distylium metzleri</i>	leaf	I	apically remotely dentate	membrana- ceous	microphyll
? <i>Viscophyllum hendriksiae</i>	leaf	III	entire	coriaceous	microphyll
<i>Hydrangea microcalyx</i>	calyx	I			
? <i>Ternstroemites maritiae</i>	leaf	I	entire	coriaceous	microphyll
<i>Symplocos deichmuelleri</i>	leaf	II	apically simple serrate	moderately coriaceous	microphyll
<i>Trachelospermum kelleri</i>	leaf	II	entire	coriaceous	nanophyll, microphyll
<i>Trachelospermum steiningeri</i>	leaf	II	entire	moderately coriaceous	microphyll
<i>Oleinites altorhenana</i>	leaf	II	entire	moderately coriaceous	notophyll
<i>Oleinites rauenbergensis</i>	leaf	II	entire	coriaceous	nanophyll
<i>Pungiphyllum cruciatum</i>	leaf	I	deeply lobate, lobes spiniform	? membrana- ceous	microphyll
<i>Dicotylophyllum badense</i>	leaf	I	entire	coriaceous	? microphyll
<i>Dicotylophyllum oechsleri</i>	leaf	I	coarsely serrate, teeth spiny	coriaceous	microphyll
<i>Dicotylophyllum vesiculaeferens</i>	leaf	II	entire	coriaceous	microphyll
<i>Dicotylophyllum zieglerei</i>	leaf	I	entire	moderately coriaceous	microphyll
<i>Dicotylophyllum</i> sp.	leaf	I	entire	moderately coriaceous	microphyll
<i>Cladites vesiculaeferens</i>	axis	III			

Hydrangeaceae, ? Pentaphragmaceae, Symplocaceae, Apocynaceae, and Oleaceae – are represented by one or two species. The most abundant fossil species are *Platanus neptuni*, followed by *Daphnogene cinnamomifolia*, *Tetraclinis salicornioides*, *Laurophyllum pseudoprinceps*, and *Palmacites lamanonis*, while other species are represented by one or few remains only. Remains of ferns are extremely rare and not diverse: *Lygodium kaulfussii*, Filicopsida sp. Cycads are represented by a single leaflet fragment of

*Ceratozamia floersheimensis*. Conifer diversity is rather high (12 species), of which *Pinus* (two five-needled, one three-needled, three two-needled species, and two species based on cones) and *Tetraclinis salicornioides* (twig fragments) are well represented, whereas *Taxodium* sp. is documented by three, and *Doliosstobus* and *Sequoia* each by only a single foliated twig remain. Remarkably, in the Rauenberg assemblage, Fagaceae are almost absent except for a single leaf of *Eotrigonobalanus furcinervis*

*f. haselbachensis*, and the record of Pentaphyllaceae is scarce and the remains ambiguous (? *Ternstroemites maritiae*). Fan palm remains are more common than those of feather palms, and ? Calamoideae are represented by a single strongly armed remain.

Thirty-nine terrestrial woody angiosperm taxa are represented by simple entire-margined or mainly minutely serrate leaves. Two taxa, *Pungiphyllum cruciatum* and *Dicotylophyllum oechsleri*, show large spiny teeth. The leaf texture of more than two thirds of the dicots is coriaceous or moderately coriaceous, while less than one third have membranaceous leaves. The prevailing laminar size of the foliage is microphyll (67%), followed by notophyll (13%), nanophyll (8%), and mesophyll (1%). Cuticle preservation is reasonably good, but fungal infection is very common. The stomata are often masked by penetrating fungi, and the hyphae network disturbs the cuticular picture.

## DISCUSSION

### TAPHONOMY

The flora of Rauenberg derives from mainly well-bedded to laminated clay to siltstones of marine origin (Bodenheim Formation). Terrestrial plant fossils are not condensed in layers or lenses but are found widely scattered, as is characteristic for marine sediments. Fragmentation of the plant material, resulting in leaves lacking apex or/and base, is common, indicating mechanical stress; relatively small-leaved taxa (predominant laminar size microphyll) comprise >70%. *Tetraclinis salicornioides*, one of the few abundant species, is represented mainly by single whorls, while articulate twigs are extremely rare. Although foliage of *Platanus neptuni* is by far the most common, not a single remain is reminiscent of a plane tree inflorescence or infructescence. These peculiarities, along with high species diversity but low representation of most taxa, indicate transport from the growing site to the final place of burial: that is, a highly allochthonous plant assemblage. Fungal infection of the leaf material may have started already prior to abscission; the often strong degree of infection points to a certain time span between leaf abscission and final burial. The allochthonous deposition may explain the rarity of Fagaceae

(a single leaf of *Eotriginobalanus furcinervis f. haselbachensis*) and both the scarcity and ambiguity of the Pentaphyllaceae (? *Ternstroemites maritiae*). The extremely low representation of foliage of deciduous woody taxa may also partly reflect mechanical stress during transport. Nevertheless, the absence of the respective winged fruits (except for a single, poorly preserved remain of *Craigia brononii*, *Betula dryadum* and involucres of *Engelhardtia macroptera*) may be interpreted as low representation of such taxa in the vegetation. The transport distance remains open, but the basal Bodenheim Formation was deposited further away from the coast than its near-shore equivalent, the Alzey Formation (Grimm 2005). Rather shallow depositional depth was widely assumed by different authors (Weiler 1966, Micklich & Hildebrandt 2010, Micklich et al. 2009), but Grimm et al. (2002) argued for about 200 m water depth. Based on a comparison with modern relatives of the fish taxa, Maxwell et al. (2016) again propose moderately shallow conditions. The rich and diverse plant record is more supportive of the latter interpretation.

### ALGAE AND MONOCOTYLEDONS

Band-like, thin, brownish, hardly carbonised fragments not showing venation represent marine algae (*Laminarites latus*, *Thallites multifidus*). Parallel-veined carbonised plant tissue was erroneously interpreted as “reeds” (Micklich & Hildebrandt 2010). Cuticular analysis revealed that such specimens represent highly fragmented palm foliage. A single remain turned out to represent the cycad *Ceratozamia floersheimensis*. No remains of reeds and sedges (Cyperaceae) or grasses (Poaceae) have been encountered. The presence of the sirenian “*Halitherium*” suggests the presence of seagrass meadows in the surrounding regions (Reich et al. 2015, Maxwell et al. 2016), but no seagrasses (Zosteraceae) have been detected among the rich fossil material.

### VEGETATION ANALYSIS AND RECONSTRUCTION

Based on the autecology of modern relatives, autecological traits are inferred for the fossil species (Tab. 2). Probably more than 60% of the woody angiosperms were evergreen, while presumably deciduous taxa make up less

than 20%; for about the same percentage it remains unclear whether they regularly shed their foliage. Deciduous representatives were Betulaceae vel Ulmaceae sp., *Carya*, possibly *Engelhardia*, *Platanus neptuni*, *Populus germanica*, and possibly *Sloanea*. The presence of winged fruits of *Betula dryadum* and *Craigia brononii* as well as the calyx remain of *Hydrangea microcalyx* indicate higher diversity of deciduous taxa than indicated by leaf remains.

Except for ferns, all terrestrial taxa reported (64) were woody. About 35% presumably were tall trees or trees. About the same percentage encompasses taxa that likely were small trees or shrubs, and >10% may represent lianas or climbers. Presumably anemophilous and zoo-philous woody taxa are almost equally represented (about 40% each). Based on the hummingbirds recorded from Rauenberg (Mayr 2004), Apocynaceae, Loranthaceae, and Pentaphyllaceae may be considered to be possibly bird-pollinated taxa. Taxa with a presumably zoochorous fruit vector predominate over anemochorous ones (>40% versus about 35%) and about 10–15% were possibly dischorous or autochorous.

The IPR vegetation analysis (Kovar-Eder & Kvaček 2008, Teodoridis et al. 2011b) enables a semiquantitative evaluation of the zonal vegetation type. This approach has been successfully tested and calibrated by application to modern vegetation in China and Japan (Teodoridis et al. 2011a). For the Rauenberg fossil flora, this analysis indicates broad-leaved evergreen forests as zonal vegetation (BLE-component 49%, BLD-component 19%, SCL+LEG component 13–14%, conifers 12% of all zonal taxa) (Appendix 2). This result must be considered together with the allochthonous deposition of the Rauenberg assemblage (see section “Taphonomy”), which may have led to a certain overrepresentation of the BLE and SCL+LEG components at the cost of the BLD component. Nevertheless, the here-presented result is regarded as robust for two reasons: the threshold of the BLE component for broad-leaved evergreen forests is >40% (Teodoridis et al. 2011a) and the number of presumably zonal taxa is high as compared to other fossil leaf assemblages.

Sociological and physiognomical comparisons consistently indicate affinity to evergreen sclerophyllous broad-leaved forest (sensu Wang 1961; i.e. broad-leaved evergreen forest

in the sense of IPR-vegetation analysis) as the most likely zonal vegetation type. Today, Fagaceae, Lauraceae, Pentaphyllaceae, and Magnoliaceae are dominant in this forest type and diversity is very high on the species level (Wang 1961). Numerous species (especially of Fagaceae) are closely allied, indicating rather recent diversification. Such diversification may be assumed due to the hybridisation fidelity of modern oaks, which was discussed recently by Kovar-Eder et al. (2015).

Evergreen taxa with coriaceous, ovate to lanceolate, either entire-margined or minutely serrate leaves are dominant in this forest type. Broad-leaved deciduous taxa and conifers do occur but are not important, except for some hardwoods in ecotones and also pines in successional series. Palms do occur but are less prominent than in rain forests (Wang 1961). Regarding composition, Rauenberg differs from evergreen sclerophyllous broad-leaved forest (sensu Wang 1961) in that only the diversity of Lauraceae is comparable, while Fagaceae and Pentaphyllaceae are hardly represented and Magnoliaceae are lacking. This may be linked to taphonomic bias caused by transport prior to deposition. This interpretation is supported by the presence of evergreen Fagaceae (3 species) and Pentaphyllaceae (2 species) in the nearby flora of Flörsheim (see section “The flora of Rauenberg in the European context”). In this context the evidence of *Ceratozamia*, *Platanus neptuni*, *Sloanea*, and *Trachelospermum* in Rauenberg is highly relevant. *Ceratozamia* is restricted to Central America (Mexico, Belize and Guatemala) today, where it occurs in mountains (800–1800 m) extending to lowlands; ecologically it ranges from tropical rain forests and less humid broad-leaved to seasonally dry forests with oaks and pines (Jones 1993). The relict species *Platanus kerrii*, which is regarded as an ecological equivalent of *P. neptuni*, occurs in Vietnam and Laos. Modern representatives of *Sloanea*, as opposed to the fossil species, thrive in SE China and Vietnam to Thailand (Kvaček & Hably 2001). Evidently, a comparison to modern vegetation types is limited in terms of composition.

For Rauenberg, the attempt to reconstruct the vegetation is based on the autecology of modern relatives and a comparison with modern vegetation. The diversity and abundance of pines and palms indicate open near-coastal pine forests with palms on sandy soils. This

**Table 2.** Similar living relatives of the recorded terrestrial taxa, physiology derived from modern relatives: leaf physiology, growth form, primary pollination type, and primary dispersal mechanism; small tree < 15 m, tall tree > 15 m

Taxon	Similar living relative	Inferred leaf physiology	Growth form	Primary pollination type	Primary dispersal mechanism
<b>Ferns</b>					
<i>Lygodium kaulfussii</i>	<i>Lygodium</i>	–	climber	–	–
Filicopsida sp.	?	–	–	–	–
<b>Cycads</b>					
<i>Ceratozamia floersheimensis</i>	<i>Ceratozamia kuestleriana</i> and allies	evergreen	small shrub	zoophilous	endozoochorous
<b>Conifers</b>					
<i>Doliosstrobilus taxiformis</i> ? <i>taxifomis</i>	Araucariaceae/ Taxodioideae	evergreen	tall tree	anemophilous	anemochorous
<i>Sequoia abietina</i>	<i>Sequoia sempervirens</i>	evergreen	tall tree	anemophilous	anemochorous
<i>Taxodium</i> sp.	<i>Taxodium</i>	deciduous	tall tree	anemophilous	anemochorous
<i>Tetraclinis salicornioides</i>	<i>Tetraclinis articulata</i>	evergreen	small tree or shrub	anemophilous	anemochorous
<i>Pinus (Strobilus)</i> sp. (5-needled)	<i>Pinus</i>	evergreen	tall tree	anemophilous	anemochorous
<i>Pinus</i> sp. (3 sp.) (2-needled)	<i>Pinus</i>	evergreen	tall tree	anemophilous	anemochorous
<i>Pinus</i> sp. (3-needled)	<i>Pinus</i>	evergreen	tall tree	anemophilous	anemochorous
<i>Pinus (Pinus)</i> cf. <i>thomasiana</i>	<i>Pinus</i>	evergreen	tall tree	anemophilous	anemochorous
<i>Pinus engelhardtii</i>	<i>Pinus</i>	evergreen	tall tree	anemophilous	anemochorous
<b>Angiosperms</b>					
<i>Actinodaphne pseudogermari</i>	<i>Actinodaphne</i>	evergreen	tree or shrub	entomophilous	endozoochorous
<i>Daphnogene cinnamomifolia</i>	? <i>Cinnamomum camphora</i>	evergreen	tall tree	entomophilous	endozoochorous
<i>Laurus abchasica</i>	<i>Laurus nobilis</i> and <i>L. azorica</i>	evergreen	small tree or shrub	entomophilous	endozoochorous
<i>Laurophyllum kinkelini</i> – complex	Lauraceae	evergreen	tree	entomophilous	endozoochorous
<i>Laurophyllum pseudoprinceps</i>	Ocotea	evergreen	tree	entomophilous	endozoochorous
<i>Laurophyllum rauenbergense</i>	Lauraceae	evergreen	tree	entomophilous	endozoochorous
<i>Laurophyllum</i> sp. A–C (3)	Lauraceae	evergreen	tree or shrub	entomophilous	endozoochorous
<i>Palmacites lamanonis</i>	Arecaceae	evergreen	tree or shrub	entomophilous	endozoochorous
<i>Sabalites major</i>	Arecaceae	evergreen	tree or shrub	entomophilous	endozoochorous
<i>Phoenicites</i> sp.	Arecaceae	evergreen	tree or shrub	entomophilous	endozoochorous
? <i>Calamoideae</i> gen. et sp. indet.	Arecaceae	evergreen	tree or shrub	entomophilous	endozoochorous
Arecaceae gen. et sp. indet.	Arecaceae	evergreen	tree or shrub	entomophilous	endozoochorous
<i>Platanus neptuni</i>	<i>Platanus kerrii</i>	deciduous	tall tree	anemophilous	anemochorous
? <i>Buxus egeriana</i>	<i>Buxus</i> in SE-Asia	evergreen	shrub or small tree		auto-/endo- zoochorous
<i>Eotrigonobalanus furcinervis</i> f. <i>haselbachensis</i>	<i>Trigonobalanus verticillatus</i>	evergreen	tall tree	anemophilous	dyschorous
<i>Betula dryadum</i>	<i>Betula</i>	deciduous	tree (or shrub)	anemophilous	anemochorous
Betulaceae vel Ulmaceae gen. et sp. indet.	Betulaceae, Ulmaceae	deciduous	tree (or shrub)	anemophilous	anemo-/dyscho- rourous
<i>Comptonia difformis</i>	<i>Comptonia peregrina</i>	deciduous	shrub	anemophilous	dyschorous
<i>Myrica</i> cf. <i>lignitum</i>	<i>Myrica</i>	? evergreen	shrub or small tree	anemophilous	endozoochorous
<i>Myrica longifolia</i>	<i>Myrica</i>	evergreen	shrub or small tree	anemophilous	endozoochorous
<i>Myrica obliquifolia</i>	<i>Myrica</i>	evergreen	shrub or small tree	anemophilous	endozoochorous
<i>Carya fragiliformis</i>	<i>Carya</i>	deciduous	tall tree	anemophilous	dyschorous
<i>Carya quadrangula</i>	<i>Carya</i>	deciduous	tall tree	anemophilous	dyschorous
<i>Engelhardia orsbergensis</i> / <i>macroptera</i>	<i>Engelhardia serrata</i> , <i>Oreomunnea mexicana</i>	deciduous, semi- evergreen, evergreen	tall tree	anemophilous	anemochorous

Table 2. Continued

Taxon	Similar living relative	Inferred leaf physiology	Growth form	Primary pollination type	Primary dispersal mechanism
? <i>Berchemia altorhenana</i>	<i>Berchemia</i>	deciduous, evergreen	climber or small to medium-sized tree	entomophilous	endozoochorous
? <i>Leguminocarpon</i> sp.	Fabaceae	deciduous, evergreen	tree	entomophilous	auto-/zoochorous
<i>Sloanea artocarpites</i>	<i>Sloanea</i> in SE-Asia	evergreen	tall tree	entomophilous	endozoochorous
<i>Sloanea olmediaefolia</i>	<i>Sloanea sinensis</i>	evergreen	tall tree	entomophilous	endozoochorous
<i>Populus germanica</i>	<i>Populus</i>	deciduous	tall tree	anemophilous	anemochorous
<i>Craigia bronnii</i>	<i>Craigia yunnanensis</i> , <i>C. kwangsiensis</i>	deciduous	small tree	anemo- / entomophilous	anemochorous
<i>Distylium metzleri</i>	<i>Distylium</i>	evergreen	shrub or small tree	?	autochorous
? <i>Viscophyllum hendriksiae</i>	Loranthaceae	evergreen	shrub, tree, liana	entomo-/ ornithophilous	zoochorous
<i>Hydrangea microcalyx</i>	<i>Hydrangea</i>	deciduous, evergreen	shrub, small tree or climber	entomophilous/ autophilous?	anemochorous
? <i>Ternstroemites maritiae</i>	Pentaphyllaceae (former Theaceae)	evergreen	tree or shrub	entomo-/ornithophilous	endozoochorous
<i>Symplocos deichmuelleri</i>	<i>Symplocos</i>	evergreen	tree or shrub	entomophilous	endozoochorous
<i>Trachelospermum kelleri</i>	<i>Trachelospermum</i>	evergreen	liana	entomophilous	anemochorous
<i>Trachelospermum steiningeri</i>	<i>Trachelospermum</i>	evergreen	liana	entomophilous	anemochorous
<i>Oleinites altorhenana</i>	Oleaceae	deciduous, evergreen	tree, shrub, liana	?	endo-/anemochorous
<i>Oleinites rauenbergensis</i>	Oleaceae	deciduous, evergreen	tree, shrub, liana	?	endo-/anemochorous
<i>Pungiphyllum cruciatum</i>	?	?	?	?	?
<i>Dicotylophyllum badense</i>	?	evergreen	?	?	?
<i>Dicotylophyllum oechsleri</i>	?	evergreen	?	?	?
<i>Dicotylophyllum vesiculaeferens</i>	?	evergreen	?	?	?
<i>Dicotylophyllum ziegleri</i>	?	? evergreen	?	?	?
<i>Dicotylophyllum</i> sp.	?	? evergreen	?	?	?
<i>Cladites vesiculaeferens</i>	?	?	?	?	?

interpretation is supported by the Alzey Formation, which represents the near-coastal sandy facies of the basinal Bodenheim Formation and its poorly preserved plant remains (Mallison 2002). *Daphnogene cinnamomifolia* and Myricaceae possibly were also represented in these forests, along with *Ceratozamia floersheimensis*, *Carya* and *Engelhardia orsbergensis/macroptera*, and *Platanus neptuni*. Coastal pine forests bound to sandy soils do occur in a wide variety and with numerous pine species along the eastern coast of the United States, although they are regarded mainly as secondary stands there (Okuda 1994). *Cladites vesiculaeferens* and *Dicotylophyllum vesiculaeferens*, which presumably derive from one plant species which was characterised by complex ? salt-excreting glands, thrived along the coast. Gallery forests along streams probably were characterised by associations of *Platanus neptuni* along with *Daphnogene*

*cinnamomifolia*, *Laurophyllum pseudoprinceps*, Myricaceae, *Populus germanica*, *Carya*, *Hydrangea microcalyx*, and *Craigia bronnii*. Most other taxa represented by few or single remains may derive from zonal evergreen sclerophyllous broad-leaved forests. Some of the aforementioned probably were more generalists and may have thrived in these zonal forests as well, for example *Daphno cinnamomifolia*, *Engelhardia orsbergensis/macroptera*, *L. pseudoprinceps*, and *Platanus neptuni*. The ecological plasticity of *Platanus neptuni* was already discussed by Walther (1985).

#### CLIMATE

Climate estimates are based mainly on the modern occurrence of the zonal vegetation type, that is, southern regions of evergreen sclerophyllous broad-leaved forest (Wang 1961), which is assumed to be the closest analog

for the flora of Rauenberg. Additionally, the climatic requirements of most similar living relatives of taxa such as *Ceratozamia*, *Craigia*, *Platanus neptuni*, and *Sloanea* are taken into consideration. Thus, the climatic conditions are most comparable to regions in Southeast Asia and America at around 20° N latitude today. In Southeast Asia, evergreen sclerophyllous broad-leaved forests extend mainly in regions with temperate, humid, summer hot climate (Cfa climate sensu Köppen 1936, Peel et al. 2007) or temperate, winter-dry, summer hot climate (Cwa climate) (Appendix 3). In the distribution area of *Ceratozamia*, in the southernmost parts of North America and northern Central America, tropical wet and tropical monsoon climate prevails. Floristic relations of the Rauenberg flora are, however, closer to Southeast Asia than to America. Therefore, the Rauenberg climatic conditions are interpreted as being comparable to the southern limits of Cfa climate, with possible tendencies towards a drier season in winter (Cw climate) and transition to tropical monsoon (Am) or tropical winter-dry (Af) climate. The climate may be further characterised as follows: Cfa climate in transition to Cwa (and Am or Af) climate, mean annual temperature (MAT) 19–24°C, mean annual precipitation (MAP) 1300–1700 mm, mean temperature of the warmest month (WMMT) 28–29°C, mean temperature of the coldest month (CMMT) 8–14°C, mean precipitation of the wettest month (WMMP) >230 mm, mean precipitation of the driest month (DMMP) 18–38 mm, wettest month between May and October, driest month between November and March. The warm period was wetter than the cold one. The upper limit of the derived MAT range appears somewhat high even when compared to existing ones for the Eocene (e.g., Kvaček et al. 2014, Zanazzi et al. 2007). For Rauenberg, CLAMP and the Coexistence Approach (CA) have also been applied (Moraweck et al. submit.) indicating somewhat lower MAT and WMMT values, while the CMMT estimates are fairly similar to that delivered by the modern occurrence of the zonal vegetation type (Tab. 3). CLAMP and CA signal a year-round growing season. MAP and growing season precipitation delivered by the different attempts overlap, but CA points towards lower MAP than that derived by the zonal vegetation type today. Most remarkably, especially the CA, the zonal vegetation type

**Table 3.** Climate estimates derived by the application of different methods. MAT – mean annual temperature, CMMT – coldest month mean temperature, WMMT – warmest month mean temperature, MAP – mean annual precipitation, GSP – growing season precipitation, 3\_wet – mean precipitation of the 3 wettest months, 3\_dry – mean precipitation of the 3 driest months, WMMP – wettest month mean precipitation, DMMP – driest month mean precipitation

Method applied	MAT (C°)	WMMT (C°)	CMMT (C°)	MAP (mm)	GSP (mm)	3_wet (mm)	3_dry (mm)	WMMP (mm)	DMMP (mm)
Comparison with climate in southern regions of evergreen sclerophyllous broad-leaved forests in SE Asia and regions of most similar relevant modern relatives (this study)	19–24	28–29	8–14	1300–1700				> 230	18–38
CLAMP (Moraweck et al. submit.)	18.0 (1.3)	25.8 (1.7)	9.5 (2.6)		1323.0 (497)	658.2 (239)	140.4 (104)		
CA (Moraweck et al. submit.)	17.2–20.5	25.0–25.9	12.6–13.6	1217–1322				204–349	21–27
CA Mainz Basin NP 23 (Pross et al. 1998)	16–18	25–28	6–10	1000–1300					

today and, to a minor degree, also CLAMP signal considerable seasonality in precipitation.

For NP 23 in the Mainz Basin, Pross et al. (1998) estimated a Cfa-climate with lower values for temperature and precipitation (Tab. 3) but did not refer to possible seasonality. Those authors arrived at their results based on the CA applied mainly to the pollen record from the Bodenheim drillcore. These estimates were later accepted by Kvaček (2004a). The here-presented estimates for Rauenberg are based on a detailed taxonomic framework that enables correlation with a zonal vegetation type (southern regions of evergreen sclerophyllous broad-leaved forest), and the climate in the region of the occurrence of these forests today serves as a source for the climate proxy.

The here-presented estimates for Rauenberg also differ from those presented by Grimm et al. (2011), who suggested a subtropical-mediterranean climate for the Alzey Formation, the coastal equivalent of the Bodenheim Formation. The basis for their assumption is unclear. Climate proxies for early Oligocene floras from North Bohemia and adjacent parts of Germany are also generally cooler than those presented in the current context for Frauenweiler (Kvaček et al. 2014). This is based on the high diversity of broad-leaved deciduous woody taxa there. These differences are not in conflict with the present results. Rather, they reflect climatic differentiation within former Europe, where the climatic conditions along the western coast (and also southern coast) were warmer and probably exhibited a somewhat more pronounced seasonality of precipitation. The prevailing leaf size class microphyll may support this latter assumption of pronounced seasonality of precipitation.

#### THE FLORA OF RAUENBERG IN THE EUROPEAN CONTEXT

Diversified early Oligocene floras are known from marine deposits in the Upper Rhine Graben (Bodenheim Formation) and from the Paratethys region (Tard Clay Formation) as well as from the early Miocene (Ebelsberg Formation (Rupp & Ćorić 2012; formerly “Älterer Schlier”, Upper Oligocene). As for Rauenberg, these plant assemblages are characterised by highly allochthonous deposition (Kovar 1982, Kvaček 2004a, Hably & Erdei 2015). Transport of the

plant debris from the growing site to the burial place caused sorting and selection on the one hand, and on the other hand may account for a mixture of plant remains from presumably very different habitats. In contrast, early Oligocene taphocoenoses from northern Bohemia and adjacent parts of Germany (mainly Saxony) derive mainly from lacustrine deposits in the adjacent volcanic hinterland (volcanic floras sensu Kvaček & Walther 2001) or were deposited in coastal lowlands (Leipzig Embayment, Mai & Walther 1978). Sorting and selection due to transport was less severe, e.g., Seifhennersdorf (Walther & Kvaček 2007), Bechlejovice (Kvaček & Walther 2004), Haselbach Floristic Complex (Kunzmann & Walther (2012)). These general characteristics are noteworthy for the following comparisons. Floristic complexes (sensu Mai 1995) aim to characterise the development of the forest flora across Europe. The flora of Rauenberg, however, is compared here mainly to individual floras instead of floristic complexes. This provides a better basis to further develop the scheme of floristic complexes, especially regarding age correlation.

The following comparisons are performed regionally, followed by stratigraphic position.

#### FLORAS FROM THE RHINE GRABEN AND THE PARATETHYS REGION

##### Flörsheim near Mainz, Germany, Upper Rhine Graben

Unsurprisingly, the floras from Rauenberg and Flörsheim, both very diverse, deriving from the Bodenheim Formation and dated to nannoplankton zone NP 23, show closest similarities compared to the remaining European record. *Platanus neptuni* and *Daphnogene cinnamomifolia* are the most common species at both sites. Rauenberg and Flörsheim share 26 fossil species of 16 families (Tab. 4). The cycad *Ceratozamia floersheimensis* was first described from Flörsheim. Remarkable is, among others, the presence of the following taxa in Rauenberg (absent in Flörsheim): *Doliostobus taxiformis*, *Engelhardia orsbergensis* and *E. macroptera*, *Myrica obliquifolia* (rather common in Rauenberg), *Distylium*, and *Sloanea olmediaefolia*. Fagaceae and Pentaphyllaceae (three species each, some of them abundant) play a much more important role in Flörsheim than in Rauenberg, and the record

from Flörsheim includes the following taxa not discovered in Rauenberg: *Chamaecyparites hardtii* (Göppert) Endlicher, *Laurophyllum acutimontanum* Mai, *Daphnogene engelhardtii* Kvaček, 2 species of *Andromediphyllum*, *Symplocos oligocaenica* Kvaček, *Oleinites pachyphyllus* Kvaček, and *Smilax weberi* Wessel in Wessel & Weber. As in Rauenberg, also in Flörsheim broad-leaved laurophyllous species with entire or minutely serrate margin prevail over presumably deciduous modern Arcto-Tertiary taxa (sensu Kvaček 1994). Among the latter, Betulaceae are represented by leaves of three genera (*Alnus*, *Carpinus*, *Ostrya*) in Flörsheim, each with one species, but *Betula*, which is documented by a winged fruit from Rauenberg, is not among them. *Craigia* and *Hydrangea* have been detected only in Rauenberg. Mai (1995) established the Floristic Complex Nerchau-Flörsheim (see section “The flora of Rauenberg in the context of the concept of floristic complexes”).

Orsberg, Siebengebirge, Rheinland-Pfalz  
(Germany), southern margin  
of the Lower Rhenish Embayment

Based on the dating of the nearby site Rott (mammal Paleogene zone MP 30), this recently revised leaf and fruit flora is thought to be late Oligocene/early Miocene in age (Winterscheid & Kvaček 2014). The taphocoenosis from the lignites (mainly fructifications) yields an impoverished Younger Mastixioid Flora (sensu Mai 1995), while the younger taphocoenosis from bituminous oil shales represents the remnants of riparian and swamp forests. Among conifers, Orsberg and Rauenberg share *Sequoia abietina* and *Tetraclinis salicornioides*. The swamp element *Glyptostrobus europaeus* (Brongniart) Unger, represented by twigs and cones in Orsberg, underpins the differences in facies to Rauenberg. In addition to taxa shared with Rauenberg (Tab. 4), leaves of *Dombeyopsis lobata* Unger, present in Orsberg, and a single fruit of *Craigia bronniei* from Rauenberg represent a single Malvaceae species. *Laurophyllum acutimontanum* and *L. haemisphaericum* (Roselt & Schneider) Winterscheid & Kvaček occur only in Orsberg. *L. sp. 2* from Orsberg resembles the leaf SMNS P 1953/76 included in *Daphnogene cinnamomifolia* from Rauenberg. Leaf taxa not present in Rauenberg include: *Acer*, *Alnus*, *Corylopsiphyllum celtifolium* (C.O. Weber in P. Wessel & C.O.

Weber) Winterscheid & Kvaček, *Vaccinioides cf. lusatica* (Litke) Kvaček & Walther, Pentaphragmataceae (3 species), Vitaceae (2), and others of cryptic affinity.

Tard Clay Formation, Hungary,  
Paratethys region

The marine Tard Clay Formation is dated to the nannoplankton zones NP 21–23, i.e. early Oligocene. Based on maceral, biomarker as well as stable isotope composition, facies changes from marine to brackish and reverse were traced (Bechtel et al. 2012). Based on the preservation type, most terrestrial plant taxa are known by gross morphology only, and no complete inventory of revised taxa is available. This hampers a full comparison (Hably & Erdei 2015). Apart from the presence and abundance of *Platanus neptuni*, *Daphnogene cinnamomifolia* and *Tetraclinis salicornioides*, Rauenberg and the Tard Clay Formation share the occurrence of *Ceratozamia floersheimensis*, *Doliosobolus taxiformis*, and *Sloanea olmedi-aefolia* (Tab. 4). None of the Lauraceae (*Laurophyllum*) identified based on cuticles from the Tard Clay Formation occur at Rauenberg. Contrary to Rauenberg, *Eotrigonobalanus furcinervis* is very common. Taxa characteristic of the Tard Clay Formation such as *Ziziphus zizyphoides* (Unger) Weyland, *Cedrelospermum aquense* (Saporta) Saporta, *Raskya vetusta* (Ettingshausen) Manchester & Hably, *Kydia kraeuselii* (Rásky) Hably and the diversity of putative legumes distinguish this early Oligocene flora from the Hungarian part of the Paratethys region from that of the Upper Rhine Graben (Rauenberg and Flörsheim).

Linz, Austria, Central Paratethys

This flora derives from the Ebelsberg Formation, formerly “Älterer Schlier” (Kovar 1982). Nannoplankton indicates zone NN 1, i.e. Lower Miocene (Rupp & Ćorić 2012). Similarly to Rauenberg, the terrestrial plant remains occurred widely scattered in the sediment and were associated with both marine and terrestrial organism groups (Kovar 1982). In both regions, near-coastal sandy sediments are developed (Alzey Formation in the Upper Rhine valley, Linzer Sande along the Paratethys coast around Linz). Rauenberg and Linz share, among others, the diversity of pines and fan palms (Tab. 4), indicating near-coastal

pine forests on sandy soils, and the abundance of *Platanus neptuni*, *Daphnogene cinnamomifolia* and *Tetraclinis salicornioides*. Except for numerous taxa present solely in Rauenberg, major distinguishing features are the presence of *Cunninghamia miocenica* Ettingshausen, *Trigonobalanopsis rhamnoides* (Rossmmaessler) Kvaček & Walther, *Acer*, *Fagus*, Betulaceae (2), and Ulmaceae (2) only in Linz. Some of these discrepancies presumably reflect differences in age, such as the absence of *Doliosstrobilus* in Linz or the absence of *Cunninghamia* in Rauenberg.

FLORAS FROM THE LEIPZIG EMBAYMENT  
(GERMANY) AND THE VOLCANIC FLORAS  
FROM THE ČESKÉ STŘEDOHOŘÍ MOUNTAINS,  
NORTH BOHEMIA (CZECH REPUBLIC)  
AND SAXONY (GERMANY)

The Floristic Complex Haselbach,  
Leipzig Embayment, Weissenster Basin,  
Saxony, Sachsen-Anhalt, Germany

The Floristic Complex Haselbach (Mai & Walther 1978) comprises a suite of mainly parautochthonous assemblages reflecting different, prevailing intrazonal habitats such as swamp forests, riparian forests, pioneer vegetation and fluvio-lacustric aquatic assemblages of the extended near-coastal lowland in the Leipzig Embayment (Kunzmann & Walther 2012). The stratigraphic assignment to the Lower Oligocene is based on palynological data (occurrence of *Boehlenpollis hohlhii* Krutzsch; Krutzsch 2011). Plants of lacustric, swampy, and fluvial settings are highly diversified both in the leaf and fruit record, whereas zonal taxa are mainly restricted to the fruit record (Mai & Walther 1978). Conifers are very diverse, including numerous taxa of wetland and swamp environments as well as *Tsuga* and *Cephalotaxus*, while *Doliosstrobilus*, which is present in Rauenberg, has not been recorded (Tab. 4). Generally, broad-leaved deciduous woody angiosperms are diversified in the Floristic Complex Haselbach, while neither *Alnus*, *Carpinus*, *Salix*, *Acer* or *Liquidambar*, to mention some, have been encountered in Rauenberg. Shared woody angiosperms between Rauenberg and the Floristic Complex Haselbach are mainly restricted to coriaceous ones that probably preferred intrazonal settings. This includes fan palms, *Daphnogene*

*cinnamomifolia*, *Laurophyllum pseudoprinceps*, *Platanus neptuni*, and *Populus germanica*. The latter two do occur in both regions abundantly, but *Eotrigonobalanus furcinervis* is common only in the Haselbach Floristic Complex. Both floras further share the presence of *Distylium*, *Symplocos* and palms of putative calamoid affinity, although all are represented by different species. Lauraceae are much less diversified in the Floristic Complex Haselbach (4 species) than in Rauenberg (10). Remarkable is the absence of *Ceratozamia*, *Craigia*, *Hydrangea*, *Sloanea*, *Trachelospermum*, and Oleaceae from the Floristic Complex Haselbach.

Bechlejovice, České středohoří Mountains,  
Czech Republic

This fossil leaf assemblage derives from diatomites deposited in a lake that had developed in a volcanogenic environment. Radiometric dating of a tephrite intrusion ( $26.8 \pm 1.34$  Ma) indicates an older age of this flora than this date. Due to the presence of archaic taxa Kvaček & Walther (2004) consider this flora to derive from the basal part of the Lower Oligocene and assign it to the Floristic Complex Haselbach – Valeč. The plant remains document flora and associations in the nearby lake surroundings. The lack of cuticles hampers floristic comparisons. In Bechlejovice, the only available conifer is *Torreya*. Among angiosperms, *Platanus neptuni* does occur but it is extremely rare. Bechlejovice and Rauenberg share *Carya*, *Craigia brononii*, *Comptonia difformis*, *Laurophyllum pseudoprinceps*, *Pungiphyllum cruciatum*, *Sloanea artocarpites*, and possibly also Zamiaceae (Tab. 4). Otherwise, Bechlejovice differs by the high diversity of broad-leaved deciduous taxa (4 genera and at least 5 species of Betulaceae, at least 4 maple species, etc.) compared to broad-leaved laurophyllous ones. It also differs by the presence of conservative taxa such as *Platanus schimperii* (Heer) Saporta & Marion, *Sterculia crassinervis* (Ettingshausen) Procházka & Bůžek, and *Haemanthophyllum*.

Kundratice, České středohoří Mountains,  
Czech Republic

The flora of Kundratice was deposited in a volcanic lake. Radiometrical dating of the base of the superimposed basalt provided an

**Table 4.** Floristic comparisons. Taxa in the flora of Rauenberg compared to Oligocene European sites

Taxa in Rauenberg	Flörsheim (Kvaček 2004a)	Orsberg (Winterscheid & Kvaček 2014)	Tard Clay (Hably 1979, Hably & Erdei 2015)	Linz, Austria (Kovar 1982)	Haselbach Complex (Mai & Walther 1978, Kunzmann & Walther 2012)
Microthyriaceae				+	
<i>Cystoseirites communis</i>				<i>C. altoaustriacus</i>	
<i>Thallites multifidus</i>	+				
<i>Laminarites latus</i>	+				
<i>Lygodium kaulfussii</i>	+				+
<i>Filicopsida</i> sp.					
<i>Ceratozamia floersheimensis</i>	+		+		
<i>Doliosobus taxiformis</i>			+		
<i>Sequoia abietina</i>		+	<i>S. langsdorfi</i>	+	+
<i>Taxodium</i> sp.	+		<i>Taxodium dubium</i>	+	<i>T. dubium</i>
<i>Tetraclinis salicornioides</i>	+	+	+ and <i>T. brachyodon</i>	+	+
<i>Pinus</i> ( <i>Strobus</i> ) sp. 1	+		<i>P. palaeostrobus</i>		<i>P. palaeostrobus</i>
<i>Pinus</i> ( <i>Strobus</i> ) sp. 2					
<i>Pinus</i> sp. 3	+			<i>Pinus</i> sp. (3)	<i>P. div. sp.</i>
<i>Pinus</i> sp. 4					
<i>Pinus</i> sp. 5					
<i>Pinus</i> sp. 6					
<i>Pinus</i> ( <i>Pinus</i> ) cf. <i>thomasiana</i>	+				
<i>Pinus engelhardtii</i>	+				
<i>Actinodaphne pseudogermari</i>					
<i>Daphnogene cinnamomifolia</i>	+	+	<i>D. div. sp.</i>	<i>D. sp.</i>	+
<i>Laurus abchasica</i>	+	+			
<i>Laurophyllum kinkelinii</i>	+	+			
<i>Laurophyllum</i> cf. <i>kinkelinii glabrum</i>	+				
<i>Laurophyllum pseudoprinceps</i>	+			+	+
<i>Laurophyllum rauenbergense</i>	as <i>L. cf. villense</i>				
<i>Laurophyllum</i> sp. A					
<i>Laurophyllum</i> sp. B					
<i>Laurophyllum</i> sp. C					
<i>Palmacites lamanonis</i>	+				
<i>Sabalites major</i>				<i>Sabal major</i>	<i>Sabal raphifolia</i>
<i>Phoenicites</i> sp.	as ? <i>Phoenicites</i> sp.				
? Calamoideae gen. et sp. indet.					<i>Calamus daemonorops</i>
Arecaceae gen. et sp. indet.					
<i>Platanus neptuni</i>	+		+	+	+
? <i>Buxus egeriana</i>				<i>B. egeriana</i>	
<i>Eotrigonobalanus furcinervis</i> f. <i>haselbachensis</i>	+		<i>E. furcinervis</i>		<i>E. furcinervis</i>
<i>Betula dryadum</i>					
Betulaceae vel Ulmaceae gen. et sp. indet.					
<i>Comptonia difformis</i>	as <i>C. schrankii</i>	+	<i>C. acutiloba</i>	<i>C. acutiloba</i>	cf. <i>C. acutiloba</i>
<i>Myrica cf. lignitum</i>	<i>M. lignitum</i>	<i>M. lignitum</i>		<i>M. lignitum</i>	
<i>Myrica longifolia</i>	+				+
<i>Myrica obliquifolia</i>					
<i>Carya fragiliformis</i>	<i>Carya</i> sp.				



Table 4. Continued

Taxa in Rauenberg	Flörsheim (Kvaček 2004a)	Orsberg (Winterscheid & Kvaček 2014)	Tard Clay (Hably 1979, Hably & Erdei 2015)	Linz, Austria (Kovar 1982)	Haselbach Complex (Mai & Walther 1978, Kunzmann & Walther 2012)
<i>Carya quadrangula</i>	+				+
<i>Engelhardia orsbergensis</i>		+	+	+	+
<i>Engelhardia macroptera</i>		+	+		+
? <i>Berchemia altorhenana</i>					
? <i>Leguminocarpon</i> sp.					
<i>Sloanea artocarpites</i>	+				
<i>Sloanea olmediaefolia</i>			+		
<i>Populus germanica</i>	+				+
<i>Craigia bronni</i>		<i>Dombeyopsis lobata</i>	+		
<i>Distylium metzleri</i>					
? <i>Viscophyllum hendriksiae</i>					
<i>Hydrangea microcalyx</i>		+			
? <i>Ternstroemites maritiae</i>					
<i>Symplocos deichmuelleri</i>	+	+			
<i>Trachelospermum kelleri</i>					
<i>Trachelospermum steiningeri</i>	+				
<i>Oleinites altorhenana</i>					
<i>Oleinites rauenbergensis</i>					
<i>Pungiphyllum cruciatum</i>	+				
<i>Dicotylophyllum badense</i>					
<i>Dicotylophyllum oechsleri</i>					
<i>Dicotylophyllum vesiculaeferens</i>					
<i>Dicotylophyllum zieglerei</i>					
<i>Dicotylophyllum</i> sp.					
<i>Cladites vesiculaeferens</i>					
Winged fruit or seed incertae sedis					
Spiny branch					

age of  $32.7 \pm 0.8$  Ma (Bellon et al. 1998). Thus, the flora is presumably closer in age to that of Rauenberg than that of Seifhennersdorf (see below). Conifers are relatively diverse, represented by *Cephalotaxus*, *Taxus*, *Tetraclinis*, and *Torreya*. *Tetraclinis* is the only shared one between Rauenberg and Kundratice (Tab. 4). Neither *Pinus* nor Taxodiaceae are recorded from Kundratice. Deciduous angiosperms comprise *Acer* (at least 5 species), *Alnus*, *Betula*, *Carpinus*, *Craigia*, *Cercidiphyllum*, *Ostrya*, *Tilia*, *Ulmus*, and *Zelkova*, of which Kundratice and Rauenberg share only *Betula*, *Carya*, and *Craigia*. Of five

species of Lauraceae in Kundratice and 10 in Rauenberg, both sites have only *Daphnogene cinnamomifolia* and possibly *Laurophyllum pseudoprinceps* in common. They further share *Pungiphyllum cruciatum*, *Sloanea artocarpites*, and *Symplocos deichmuelleri*. Both sites are characterised by the absence (Kundratice) or almost absence (Rauenberg) of Fagaceae. The Floristic Complex Seifhennersdorf-Kundratice (Kvaček & Walther 1998) is characterised as Mixed Mesophytic Forest vegetation with considerable diversity of broad-leaved deciduous taxa, i.e. modern Arcto-Tertiary elements.



than in Rauenberg. Besides Kundratice, Seifhennersdorf is the type locality of the Floristic Complex Seifhennersdorf-Kundratice (Kvaček & Walther 1998).

Hammerunterwiesenthal, Saxony, Germany

Age constraints of this flora were provided by radiometric dating of the basaltic tuffites there:  $30.48 \pm 0.41$  Ma (Walther 1998). Deposited in a maar lake, this plant assemblage is less diverse (25 taxa).

With its extremely low diversity of conifers – *Pinus*, *Tetraclinis salicornioides*, both present in Rauenberg (Tab. 4) – and diversity of broad-leaved deciduous taxa – *Acer* (4 species), *Alnus*, cf. *Carpinus*, cf. *Cercidiphyllum*, *Craigia*, *Hydrangea*, *Vitis* – this flora resembles most of the other volcanic floras of this region but differs from the assemblage of Rauenberg. Hammerunterwiesenthal and Rauenberg share only *Craigia* and *Hydrangea*. Out of three laurels, *Daphnogene cinnamomifolia* and probably *Laurophyllum pseudoprinceps* occur at both sites, while *L. acutimontanum* is restricted to Hammerunterwiesenthal. *Trigonobalanopsis rhamnoides* represents the only Fagaceae at this site. Fan palm findings are generally rare in the volcanic floras; a single one derives from Hammerunterwiesenthal.

Markvartice, České středohoří Mountains,  
Czech Republic

The stratigraphic position of this flora, which derives from tuffaceous diatomite and ash tuffite, is somewhat ambiguous. Based on regional geology, floristic composition and relation to other floras, such as that from Seifhennersdorf, this flora is estimated to be somewhat younger (Bůžek et al. 1976). Kvaček & Walther (2003) assign this site to the Děčín Formation which is regarded mainly late Oligocene in age. Taxodioideae are hardly documented, pines are absent, *Taxus* and *Torreya* are represented by single specimens. The only common conifer is *Tetraclinis salicornioides*. The assemblage from Markvartice differs from others of this region by the prevalence of evergreen laurophyllous taxa. The diversity of Lauraceae is almost as high as in Rauenberg. Both sites, however, share only *Daphnogene cinnamomifolia* and *Laurophyllum pseudoprinceps* (Tab. 4). Similarly to Rauenberg, *D. cinnamomifolia*, *L. pseudoprinceps*, and *Platanus neptuni* are very abundant and

*T. salicornioides* is among the common species. Among deciduous taxa, Rauenberg and Markvartice share *Betula dryadum*, *Carya*, and *Craigia bronnii*. Markvartice, however, includes further broad-leaved deciduous taxa such as *Acer* (at least 3 species), *Cercidiphyllum*, *Rosa*, and *Ulmus* not documented in Rauenberg. Both sites share the presence of *Sloanea artocarpites* and putative Oleaceae, although different species (*Oleinites maii* in Markvartice, *O. altorhenana* and *O. rauenbergensis* in Rauenberg). Documented in Rauenberg (solely by a single leaf of *Eotrigonobalanus f. furcinerervis haselbachensis*), Fagaceae records are absent at Markvartice. Mai (1995) and Kvaček & Walther (2001) assign this assemblage to the Floristic Complex Nerchau-Flörsheim.

Suletice-Berand, České středohoří Mountains,  
Czech Republic

Radiometric dating delimits the age of this flora at between  $28.3 \pm 1.4$  Ma and  $19.8 \pm 0.5$  Ma (Bellon et al. 1998). This taphocoenosis was embedded in diatomites that developed in a volcanic lake setting. The comparison is biased because cuticles are rarely preserved. Conifers are not diversified; neither pines nor Taxodioideae occur. Only *Tetraclinis salicornioides* is rather frequent (Tab. 4). Among Lauraceae (at least 4 species), *Laurophyllum acutimontanum*, which is not recorded from Rauenberg, is the most common one, followed by *Daphnogene cinnamomifolia* and *Laurophyllum pseudoprinceps*. *Platanus neptuni* is abundant. Broad-leaved deciduous taxa are less diversified than for example in Seifhennersdorf or Kundratice. Among these are *Acer* (at least 3 species), *Carpinus*, *Celtis*, *Ostrya*, *Rosa*, and *Zelkova*, none of which have been detected in Rauenberg. Suletice-Berand and Rauenberg, however, share *Carya*, *Craigia bronnii*, *Engelhardia orsebrgensis/macroptera*, *Hydrangea microcalyx*, and *Sloanea artocarpites*. Putative Oleaceae are represented by different *Oleinites* species at both sites. Kvaček & Walther (1995) assign this assemblage to the Floristic Complex Nerchau-Flörsheim.

Kleinsaubernitz, Saxony (Germany)

This rich flora derives from drill cores through maar lake deposits in which the plant-bearing sediments are 270 m thick. Based on regional geology, Kleinsaubernitz was

correlated to the Upper Oligocene (Walther 1999). This was rendered more precisely to Spore-Pollen-Paleogene zone 20G (Goth et al. 2003), corresponding to the lower Upper Oligocene (Kruttsch 2011). Conifers are very diverse (Pinaceae 3 species, Cupressaceae 5, Taxaceae 1), but Kleinsaubernitz and Rauenberg share only five-needled *Pinus*, *Sequoia abietina*, *Taxodium*, and *Tetraclinis salicornioides* (Tab. 4). Angiosperms include laurophyllous taxa as well as “modern” Arcto-Tertiary ones, each group represented about 50%. Contrary to Rauenberg, Fagaceae are very diverse (8 species), among them the archaic *Eotriginobalanus furcinervis* f. *haselbachensis* as well as *Triginobalanopsis rhamnoides* and *Fagus saxonica* Kvaček & Walther. The presence of further archaic taxa such as *Majanthemophyllum petiolatum* Weber, together with taxa known from Miocene deposits such as “*Illiciium*” *limburgense* Kräusel & Weyland and *Illipophyllum thomsonii* Kräusel & Weyland, are unique. Deciduous taxa are rather diverse (e.g. *Acer*, *Alnus*, *Betula*, *Carpinus*, *Celtis*, *Craigia*, *Ulmus*) but Kleinsaubernitz and Rauenberg share only the presence of *Betula* and *Craigia brononii*. Further taxa occurring at both sites are *Comptonia difformis*, *Sloanea artocarpites*, and *Distylium*, the latter being represented by different species. Among the floristic record from the volcanic region of North Bohemia and adjacent parts of Saxony, Kleinsaubernitz is quite peculiar, which encouraged Walther (1999) to establish the Floristic Complex Kleinsaubernitz.

#### SUMMARISING THE COMPARISON OF RAUENBERG WITH THE FLORAS FROM THE LEIPZIG EMBAYMENT AND THE VOLCANIC FLORAS FROM SAXONY AND THE ČESKÉ STŘEDOHŘÍ MOUNTAINS

From a purely floristical viewpoint the following characteristics are noteworthy: *Daphnogene cinnamomifolia*, *Laurophyllum pseudoprinceps*, *Platanus neptuni*, and *Tetraclinis salicornioides* are the taxa which are present and mostly also very abundant at almost all sites. Additionally, Rauenberg and all volcanic floras share the presence of *Craigia brononii*, which is usually an accessory element. Rauenberg is distinct by the presence of *Ceratozamia floersheimensis*, *Doliostrobos taxiformis*, *Myrica longifolia*, and *Sloanea olmediaefolia*, which indicate an affinity to floras from the

Paratethys realm. Otherwise, *M. longifolia* occurs only in the Floristic Complex Haselbach. Generally, Lauraceae (10 species), Myricaceae (4) and Areaceae (4–5) are more diverse in Rauenberg than in any of the compared floras. The diversity and relative abundance of pines at Rauenberg, versus their absence or scarcity in the volcanic floras, indirectly supports the interpretation of near-coast pine forests in Rauenberg. At all compared sites from this part of Central Europe, *Acer* is present and more or less species-diverse, while there is not even a single record from Rauenberg. The high diversity of further “modern” Arcto-Tertiary elements distinguishes all these sites from Rauenberg. The diversity of taxa with simple, coriaceous, entire-margined or minutely toothed, probably evergreen leaves in Rauenberg is not only higher than in the floras from the region of Saxony, Saxony-Anhalt and North Bohemia, but many of them have never been recorded there. The latter two arguments (differences in diversity of “modern” Arcto-Tertiary elements and in prevailing leaf physiognomy) as well as the presence of different palms in Rauenberg explain the different estimated zonal forest types, namely mixed mesophytic forest or transition from mixed mesophytic to broad-leaved evergreen forest for most of the floras from North Bohemia, Saxony and Saxony-Anhalt, but broad-leaved evergreen sclerophyllous forest for Rauenberg. The floristic complex Haselbach repeatedly was interpreted as mixed mesophytic forest (Mai & Walther 1978, 1985, Mai 1995). Only recently broad-leaved evergreen forest was predicted based on the IPR vegetation analysis (Kvaček et al. 2014). The percentage of the BLE component of zonal woody taxa is, however, lower there (42.5%) than in Rauenberg (48.6%). Regarding age correlations, the plant assemblages from Kundratice and Seifhennersdorf are probably closest to Rauenberg, but their floristic match with Rauenberg is lower than that of Markvarctice, whose age is less unambiguous.

#### THE FLORA OF RAUENBERG IN THE CONTEXT OF THE CONCEPT OF FLORISTIC COMPLEXES

The plant-bearing marine sediments (Bodenheim Formation, Hochberg Member) are well correlated biostratigraphically by nannoplankton, dinoflagellate cysts and the mammal genus *Apterodon* (Figure 1, Maxwell et al. 2016). The age is therefore limited

to the middle Rupelian, i.e. approximately >30 Ma and < 33 Ma. The stratigraphic constraints for the flora of Flörsheim are very similar (Kvaček 2004a, see also Introduction). The assemblages from Rauenberg and Flörsheim share many more taxa than any of the other compared floras. The Floristic Complex Nerchau-Flörsheim, first established by Mai (1995), was further characterised by Kvaček and Walther (2001), who included also the assemblages of Markvartice and Suletice-Berand. The radiometric constraints of Suletice-Berand between  $28.3 \pm 1.4$  Ma and  $19.8 \pm 0.5$  Ma (Bellon et al. 1998) unambiguously indicate that floristically similar assemblages are not necessarily time equivalent. Assuming the validity of the radiometric dating, Suletice-Berand needs to be excluded. The age of the assemblage from Markvartice remains somewhat ambiguous (see above) and that of Nerchau is open (Mai & Walther 1991). Therefore, the typification and definition of the respective floristic complex should exclude Nerchau. Rauenberg is to be definitely assigned to this complex. Due to the excellent stratigraphic correlation possibilities and the partly identical as well as complementary spectrum of taxa at Rauenberg, the Floristic Complex Flörsheim-Rauenberg is suggested here instead. Typification for Rauenberg: Stratum typicum: Bodenheim Formation, Hochberg Member, "Fischschiefer", NP 23, Lower Oligocene. Locus typicus: Rauenberg, Baden-Württemberg, Germany.

The concept of floristic complexes presented by Kvaček and Walther (2001) is based on a north-south gradient (Boreal Province and Paratethys Province). The flora from the Tard Clay Formation serves as the type flora of the Floristic Complex Kiscell (Mai 1995, Kvaček & Walther 2001) at the southern margin of former Europe. The stratigraphic position and similarities of the flora from the Tard Clay Formation and Rauenberg (as well as Flörsheim) regarding joint taxa are clear including taxa which are not documented from the early Oligocene of North Bohemia or adjacent parts of Germany (*Ceratozamia flörsheimensis*, *Doliosstrobos taxiformis*, *Sloanea olmediaefolia*). This implies a more complex vegetation pattern in former Europe, one in which the regional climate was influenced by marine straits, rather than a simple north-south gradient.

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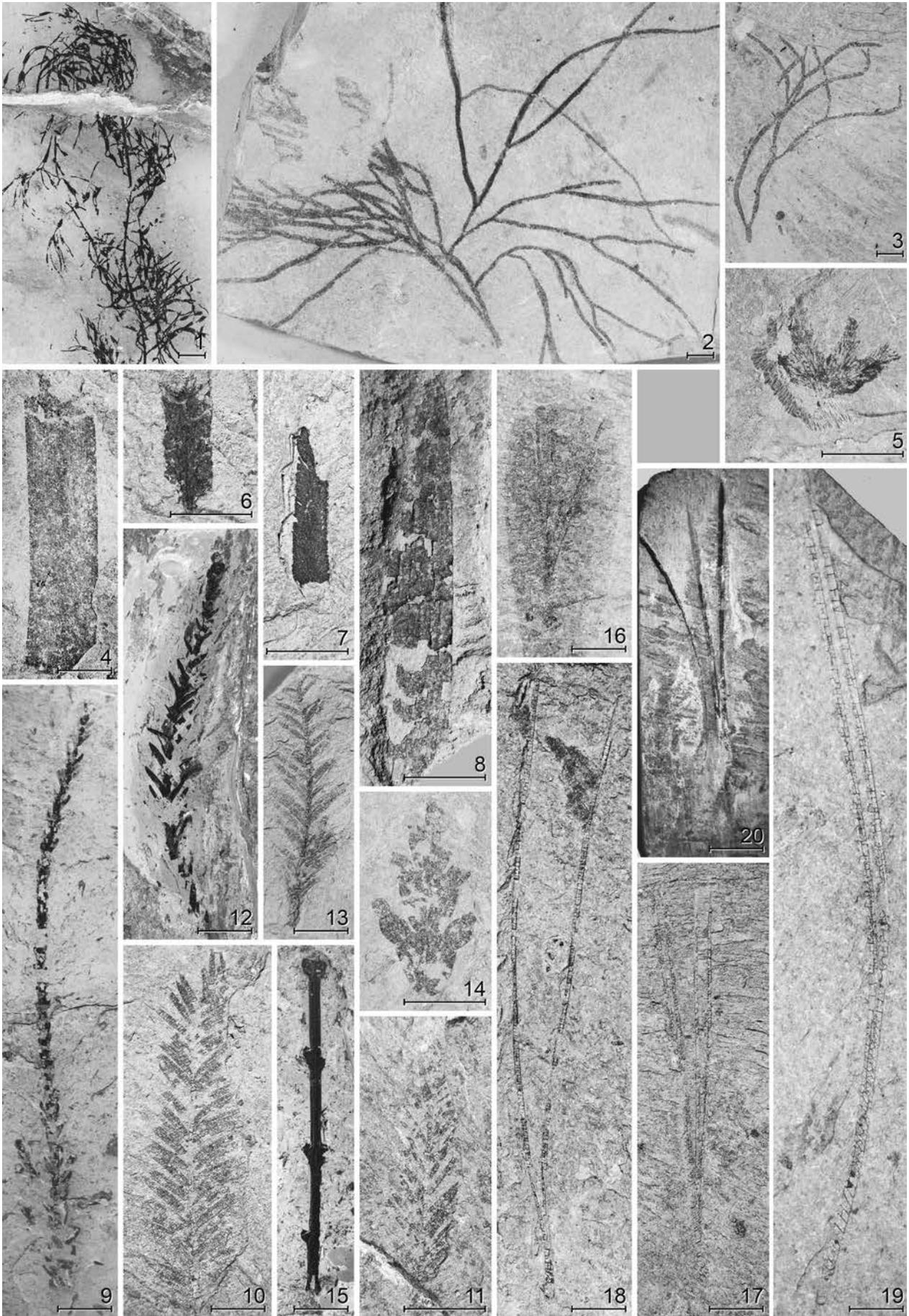
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# PLATES

## Plate 1

1. *Cystoseirites communis* Unger, SMNS P 1953/111
- 2–3. *Thallites multifidus* (Brongniart) Kvaček
  2. SMNS P 1952/1
  3. SMNS P 1952/39
4. *Laminarites latus* Engelhardt, SMNS P 1952/295
- 5–7. *Lygodium kaulfussii* Heer emend. Gardner et Ettingshausen
  5. SMNS P 1952/55
  6. SMNS P 1952/322
  7. SMNS P 1952/332
8. *Ceratozamia floersheimensis* (Engelhardt) Kvaček, SMNS P P1952/456
9. *Doliostobus taxiformis* (Sternberg) Kvaček ? taxiformis Mai & Walther, NMA 2006-104/1497
10. *Sequoia abietina* (Brongniart in Cuvier) Knobloch, NMA 2016-3/2179
- 11–13. *Taxodium* sp.
  11. SMNS P 1952/88
  12. SMNS P 1953/103
  13. SMNK 7710
- 14–15. *Tetraclinis salicornioides* (Unger) Kvaček
  14. SMNS P 1952/118
  15. SMNS P 1953/109
16. *Pinus* (Strobus) sp. 1, SMNS P 1952/292
17. *Pinus* (Strobus) sp. 2, SMNS P 1952/90
18. *Pinus* sp. 3, SMNS P 1952/460
19. *Pinus* sp. 4, SMNS P 1952/143
20. *Pinus* sp. 6, NMA 2006-111/1497

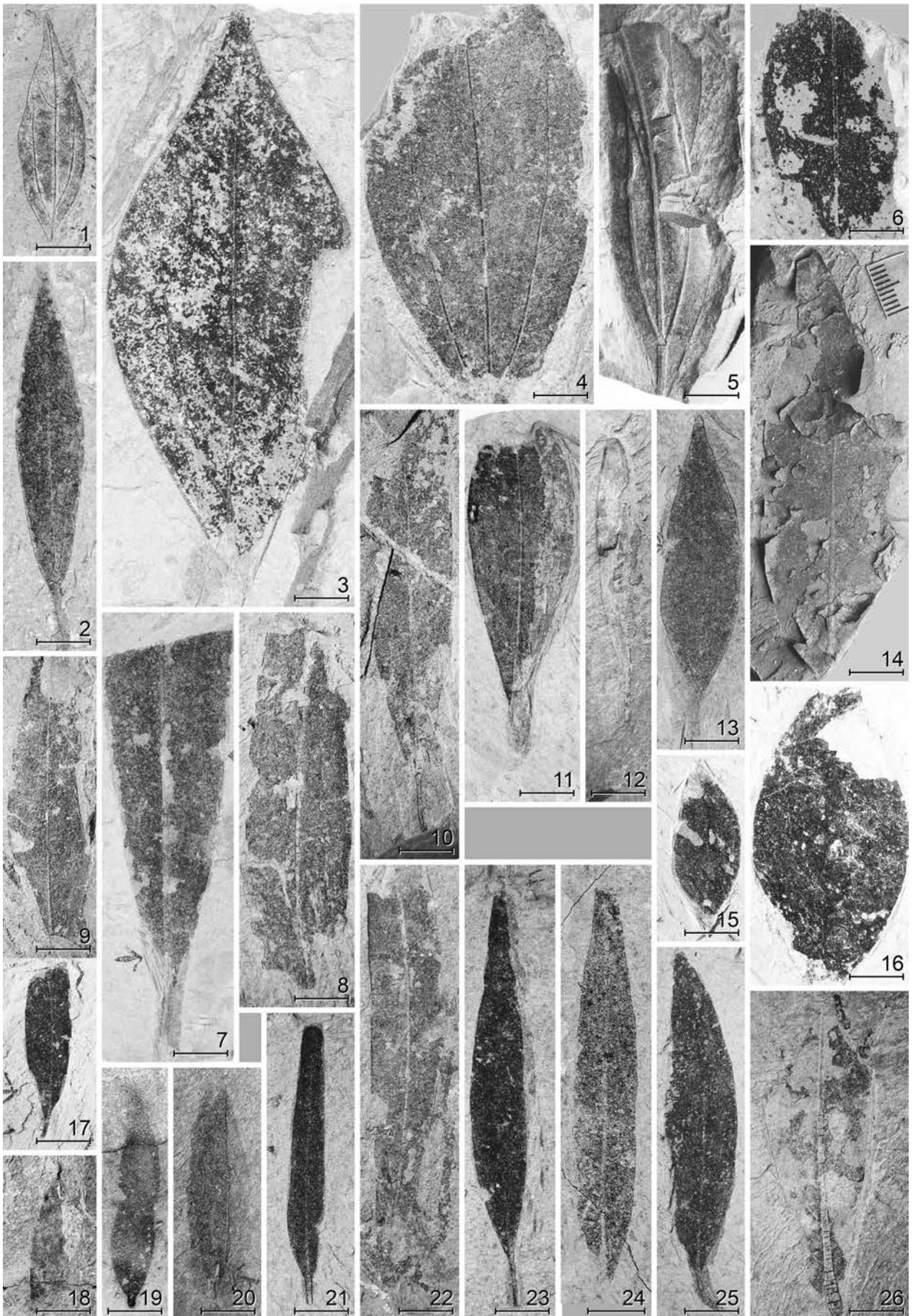
Scale bar: 10 mm



## Plate 2

- 1–6. *Daphnogene cinnamomifolia* (Brongniart) Unger
1. SMNS P 1952/71
  2. SMNS P 1953/12
  3. SMNS P 1953/8
  4. SMNS P 1953/18
  5. SMNS P1952/472
  6. SMNS P 1953/76
- 7–8. *Laurophyllum kinkelinii* (Engelhardt) Kvaček
7. SMNS P1953/64
  8. SMNS P 1952/184
- 9–11. *Laurophyllum* cf. *kinkelinii* (Engelhardt) Kvaček 2004 var. *glabrum* Kvaček
9. SMNS P 1952/396
  10. SMNS P 1952/378
  11. SMNS P 1953/87
- 12–16. *Laurophyllum pseudoprinceps* Weyland & Kilpper s.l.
12. SMNS P 1952/344
  13. SMNS P 1953/48
  14. SMNS P 1952/345
  15. SMNS P 1953/84
  16. SMNS P 1953/15A
- 17–23. *Laurophyllum rauenbergense* Kovar-Eder sp. nov.
17. SMNS P 1953/73 paratype
  18. SMNS P 1952/350
  19. SMNS P 1952/93 paratype
  20. SMNS P 1953/82 holotype
  21. SMNS P 1953/85 paratype
  22. SMNS P 1952/379
  23. SMNS P 1953/47 paratype
- 24–25. *Laurophyllum* cf. *rauenbergense* Kovar-Eder sp. nov.
24. SMNS P1952/231
  25. SMNS P 1953/59
26. *Actinodaphne pseudogermari* Walther, SMNS P 1952/17

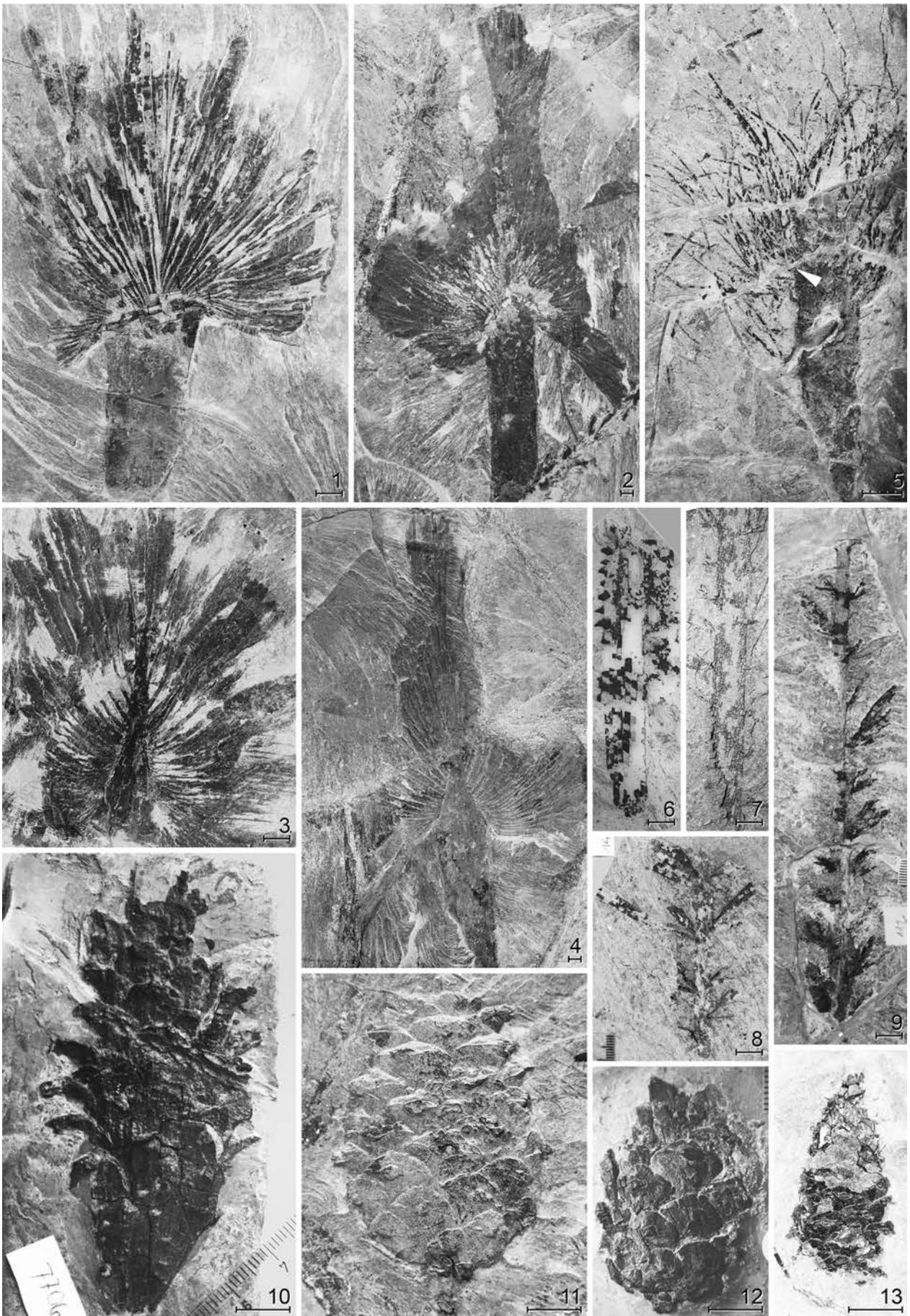
Scale bar: 10 mm



## Plate 3

- 1–2. *Palmacites lamanonis* Brongniart  
1. SMNS P 1952/175  
2. SMNS P 1953/124  
3–4. *Sabalites major* (Unger) Saporta  
3. SMNS P 1953/132  
4. SMNS P 1952/169  
5. Areaceae gen. et sp. indet., NMA 2016-2/1497, scale 50 mm  
6. ? Calamoideae gen. et sp. indet., NMA 2016-1/1497  
7–9. *Phoenicites* sp.  
7. SMNS P 1952/12  
8. SMNS P 1952/141  
9. NMA 2006-112/1497  
10. *Pinus engelhardtii* Menzel, SMNK 7706  
11–12. *Pinus* (*Pinus*) cf. *thomasiana* (Goeppert) Reichenbach  
11. SMNS P 1952/176  
12. SMNS P 1953/106  
13. *Pinus* sp., SMNS P 1952/150

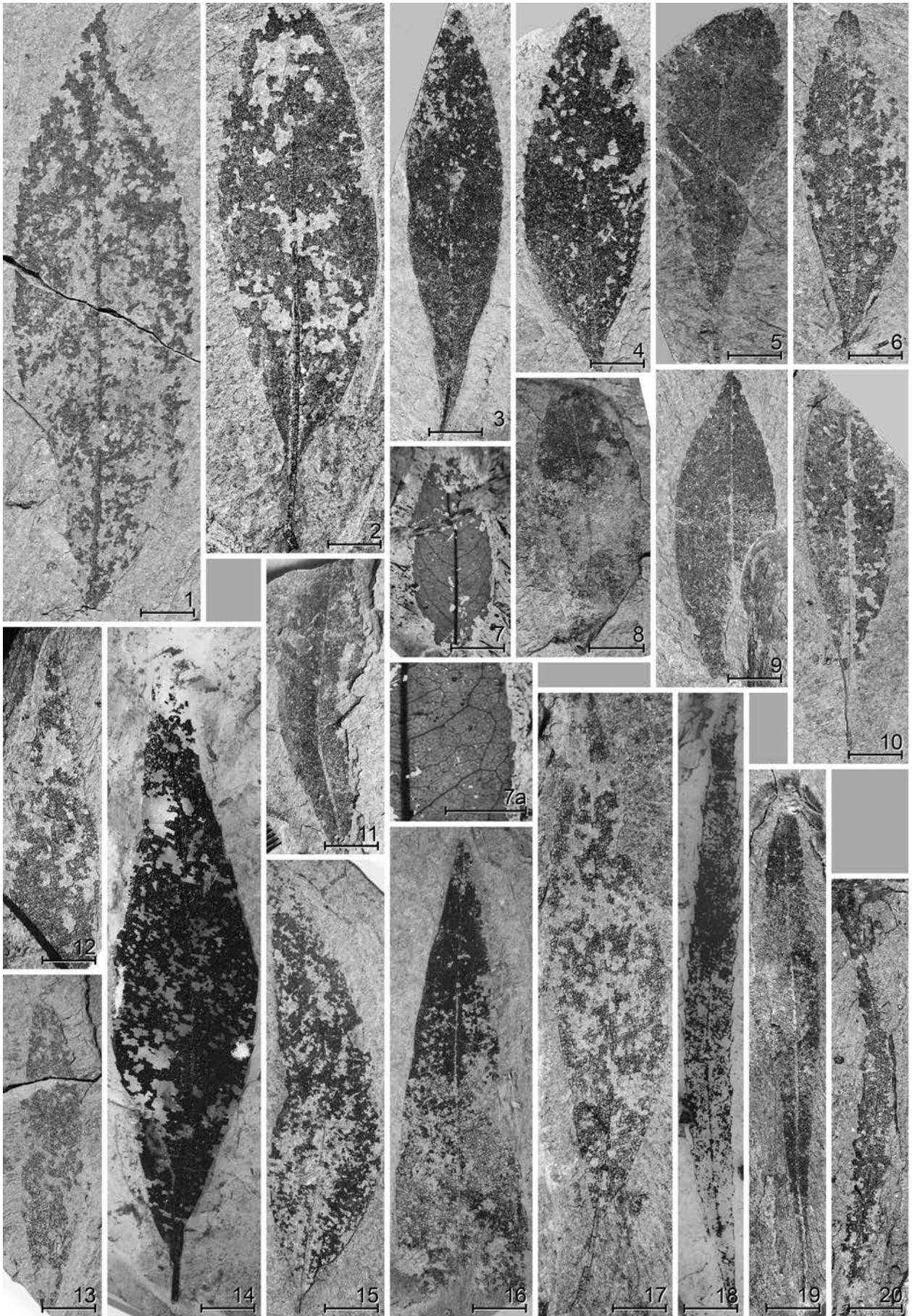
If not noted otherwise, scale bar: 10 mm



## Plate 4

- 1–10. *Platanus neptuni* (Ettingshausen) Bůžek, Holý et Kvaček
1. SMNS P 1952/32
  2. SMNS P 1952/81
  3. SMNS P 1952/14
  4. SMNS P 1952/26
  5. SMNS P 1952/220
  6. SMNS P 1952/86
  7. NMA 2006-128/1497, 7a. venation details, scale bar 5 mm
  8. SMNS P 1952/37
  9. SMNS P 1952/24A
  10. SMNS P 1952/19
11. *Myrica* cf. *lignitum* (Unger) Saporta sensu Ettingshausen & Standfest, SMNS P 1952/361
- 12–17. *Myrica obliquifolia* sp. nov.
12. SMNS P 1952/238 paratype
  13. SMNS P 1952/232 paratype
  14. SMNS P 1952/162 paratype
  15. SMNS P 1952/255 paratype
  16. SMNS P 1953/99 paratype
  17. SMNS P 1952/85 holotype
- 18–20. *Myrica longifolia* Unger
18. NMA 2006-105/1497
  19. SMNS P 1952/50
  20. SMNS P 1952/186

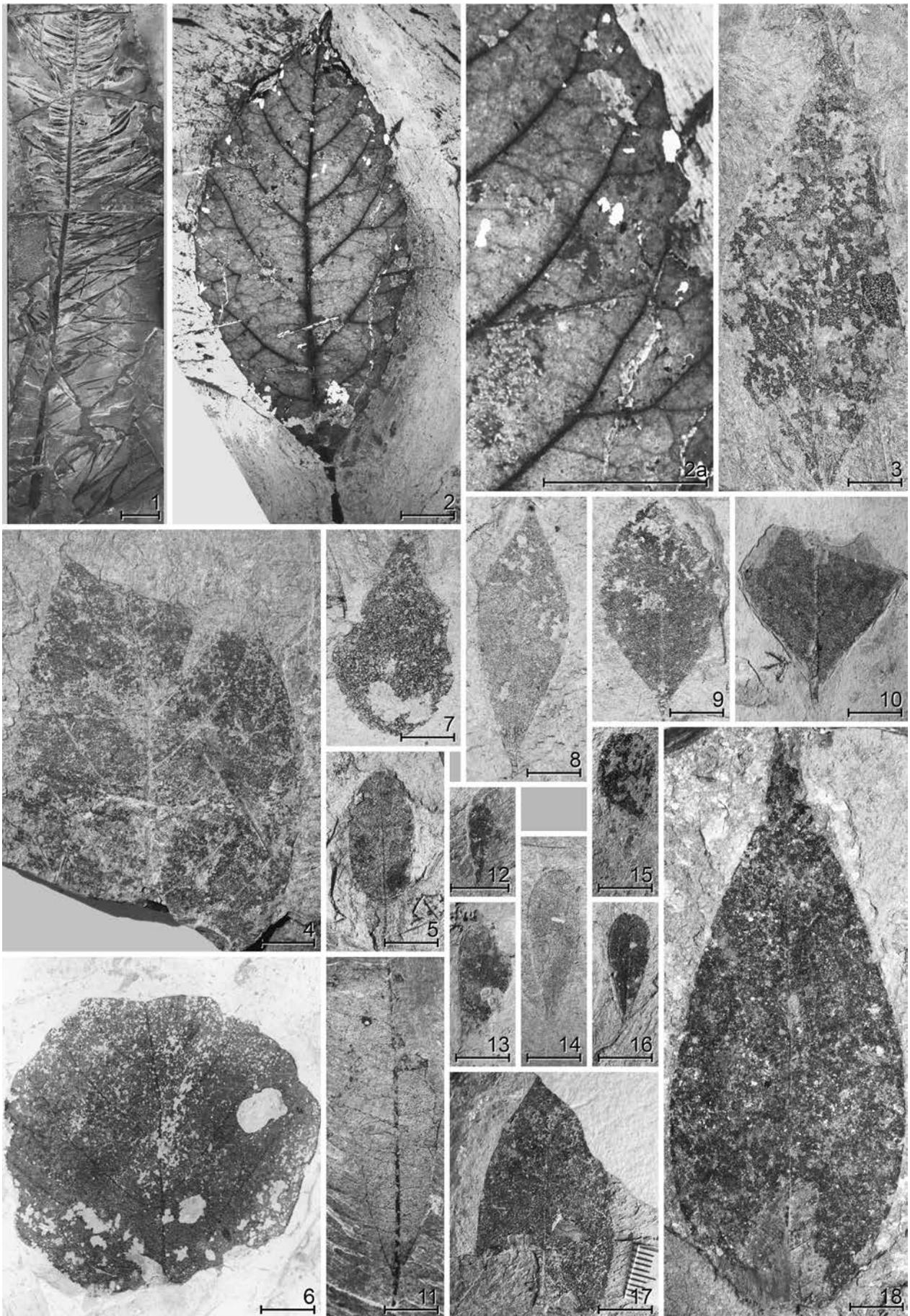
If not noted otherwise, scale bar: 10 mm



## Plate 5

1. *Phoenicites* sp., NMA 2006-180/1497, scale bar 100 mm
- 2–3. *Sloanea olmediaefolia* (Unger) Z. Kvaček & Hably
  2. NMA 2006-114/1497, 2a. venation details
  3. SMNS P 1952/340
4. *Sloanea artocarpites* (Ettingshausen) Z. Kvaček et Hably, P1952/61
5. ? *Berchemia altorhenana* Kovar-Eder sp. nov., SMNS P 1953/92, holotype
6. *Populus germanica* (Menzel) Walther, SMNK 7568
7. ? *Ternstroemites maritiae* Kovar-Eder sp. nov., SMNS P 1952/342, holotype
- 8–10. *Symplocos deichmuelleri* (Kvaček & Walther) comb. nov.
  8. SMNS P1952/62
  9. SMNS P1952/65
  10. SMNS P 1953/43
11. *Pungiphyllum cruciatum* (Al. Braun) Frankenhäuser & Wilde, NMA 2006-126/1497
- 12–14. *Oleinites rauenbergensis* Kovar-Eder sp. nov.
  12. SMNS P 1952/299 paratype
  13. SMNS P 1952/402 paratype
  14. SMNS P 1952/380 holotype
- 15–16. ? *Oleinites rauenbergensis* Kovar-Eder sp. nov.
  15. SMNS P 1952/6
  16. SMNS P 1953/93
- 17–18. *Oleinites altorhenana* Kovar-Eder sp. nov.
  17. SMNS P 1952/191 holotype
  18. SMNS P 1953/62 paratype

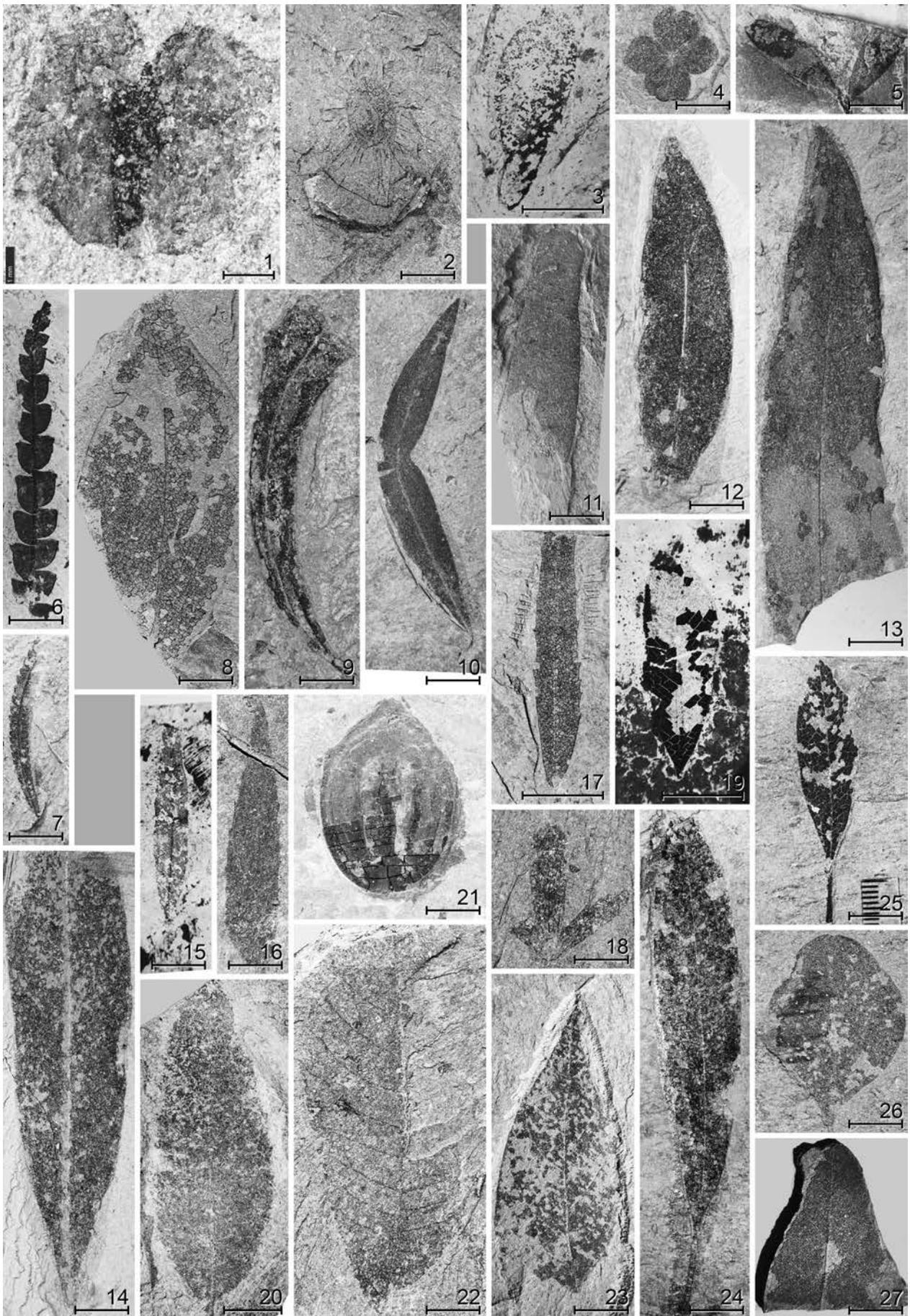
If not noted otherwise, scale bar: 10 mm



## Plate 6

1. *Betula dryadum* Brongniart, SMNK 7711, scale bar 1 mm
2. *Craigia bronnii* (Unger) Kvaček, Bůžek et Manchester, SMNK 7748
3. Winged fruit or seed incertae sedis, NMA 2006-113/1497
4. *Hydrangea microcalyx* Sieber, SMNS P 1952/145
5. ? *Leguminocarpon* sp., NMA 2006-173/1497
- 6–7. *Comptonia difformis* (Sternberg) Berry
6. SMNS P 1953/118
7. SMNS P 1952/166
8. *Laurophyllum* sp. A, SMNS P 1952/336
9. *Laurophyllum* sp. B, SMNS P 1952/47
10. *Laurophyllum* sp. C, SMNS P 1953/81
- 11–13. *Laurus abchasicus* (Kolakovskii & Shakryl) Ferguson
11. SMNS P 1952/382
12. SMNS P 1953/75
13. SMNS P 1953/65
14. *Eotrigonobalanus furcinervis* (Rossmässler) Walther & Kvaček forma *haselbachensis* (Kvaček & Walther) Kvaček & Walther in Walther, SMNS P 1953/60
- 15–17. *Engelhardia orsbergensis* (Wessel & Weber) Jähnichen, Mai & Walther
15. NMA 2006-108/1497
16. SMNK 7499
17. SMNS P 2228/1
18. *Engelhardia macroptera* (Brongniart) Unger, SMNS P 1952/154
19. ? *Buxus egeriana* Kvaček, Bůžek et Holý, NMA 2006-168/1497
20. Betulaceae vel Ulmaceae gen. et sp. indet., SMNS P 1952/437
21. *Carya quadrangula* (Kirchheimer) Leroy, SMNS P 1952/159
22. *Carya fragiliformis* (Sternberg) Kvaček & Walther, SMNS P 1952/58
23. *Distylium metzleri* Kovar-Eder sp. nov., SMNS P 1952/43 holotype
- 24–25. *Trachelospermum kelleri* Kovar-Eder sp. nov.
24. SMNS P 1953/101 paratype
25. NMA 2006–121/1497 holotype
- 26–27. *Trachelospermum steiningeri* Kvaček
26. SMNS P 1952/101
27. SMNS P 1952/366

If not noted otherwise, scale bar: 10 mm



## Plate 7

1–5. *Viscophyllum hendriksiae* Kovar-Eder sp. nov.

1. SMNS P 1952/11 paratype
2. SMNS P 1952/57 paratype
3. SMNS P 1953/70 holotype
4. SMNS P 1953/77 paratype
5. SMNS P 1952/158 paratype
6. *Dicotylophyllum zieglerei* Kovar-Eder sp. nov., SMNS P 1953/86 holotype

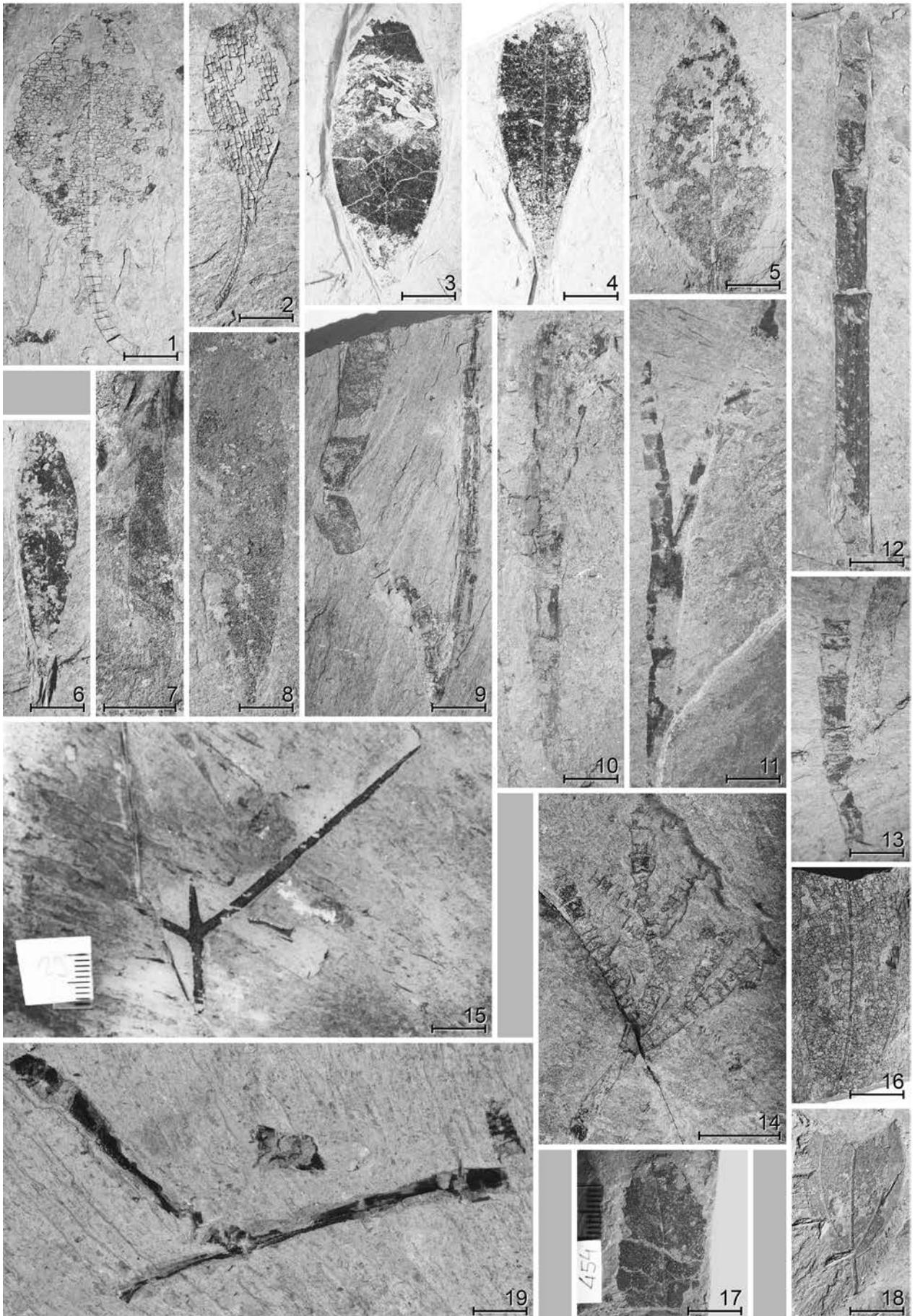
7–8. *Dicotylophyllum vesiculaeferens* Kovar-Eder sp. nov.

7. SMNS P 1952/310 holotype
8. SMNS P 1952/306 paratype

9–14. *Cladites vesiculaeferens* Kovar-Eder sp. nov.

9. SMNS P 1952/371 paratype
10. SMNS P 1952/416 holotype
11. NMA 2006-154/1497
12. SMNS P 1953/105
13. NMA 2016-4/2179
14. SMNS P 1952/87 paratype
15. Spiny branch, NMA 2006-23/1497
16. *Dicotylophyllum badense* Kovar-Eder sp. nov., SMNS P 1952/200 holotype
17. *Dicotylophyllum oechsleri* Kovar-Eder sp. nov., SMNS P 1952/454 holotype
18. *Dicotylophyllum* sp., SMNS P 1952/400
19. *Cladites vesiculaeferens* Kovar-Eder sp. nov., SMNS P 1952/104

Scale bar: 10 mm



## Plate 8

1–3. Microthyriaceae gen. et sp. indet.

Different stages of fruiting bodies on the cuticle of *Phoenicites* sp.

1. SMNS P 1952/473-1
2. SMNS P 1952/473-2
3. SMNS P 1952/473-1

4–7. *Ceratozamia floersheimensis* (Engelhardt) Kvaček

4–6. Cuticle in stoma-bearing condition, note the short rows of strongly cutinised short cells;

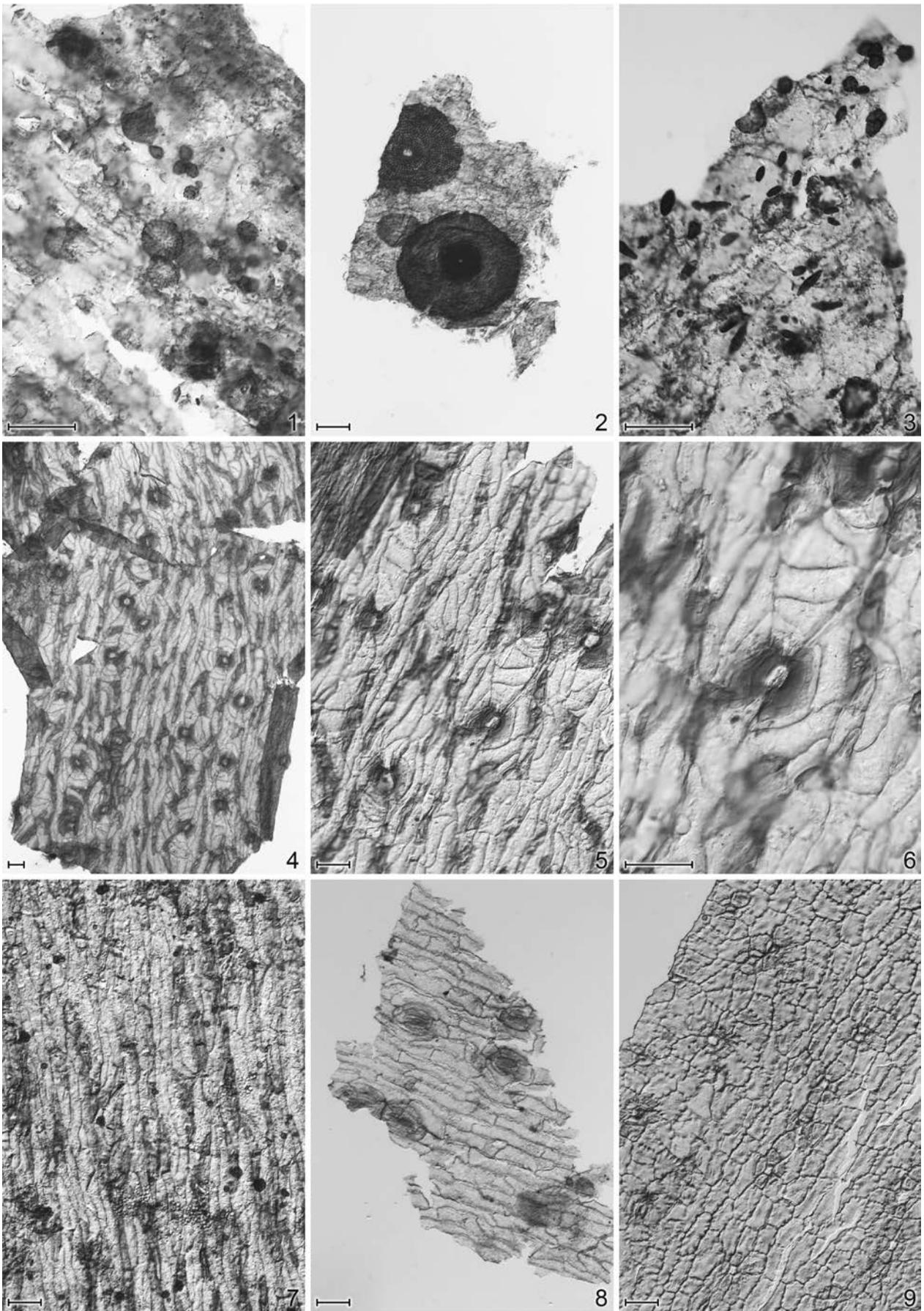
4. SMNS P 1952/456-2
5. SMNS P 1952/456-1

6. Stomata with encircling cells, polar cells very slender, remnants of guard cells still preserved, SMNS P 1952/456-1

7. Cuticle in non-stoma-bearing condition, SMNS P 1952/456-2

8. *Sequoia abietina* (Brongniart in Cuvier) Knobloch, NMA 2016-3/2179-2
9. *Tetraclinis salicornioides* (Unger) Kvaček, SMNS P 1952/194-2

Scale bar: 50 µm



## Plate 9

1–3. *Actinodaphne pseudogermari* Walther

1. Adaxial cuticle and oil glands, SMNS P 1952/17-1

2–3. Abaxial cuticle with stomata overlapped by neighbouring cells, SMNS P 1952/17-2

4–9. *Daphnogene cinnamomifolia* (Brongniart) Unger

4–5. Probable shade leaf

4. Adaxial cuticle with undulate anticlines and a single trichome base upon a lower-order vein, SMNS P 1953/8-2

5. Abaxial cuticle, largely glabrous except for a prominent trichome base, SMNS P 1953/8-1

6. Abaxial cuticle, trichome bases with thickened polar rim, SMNS P 1953/76-2

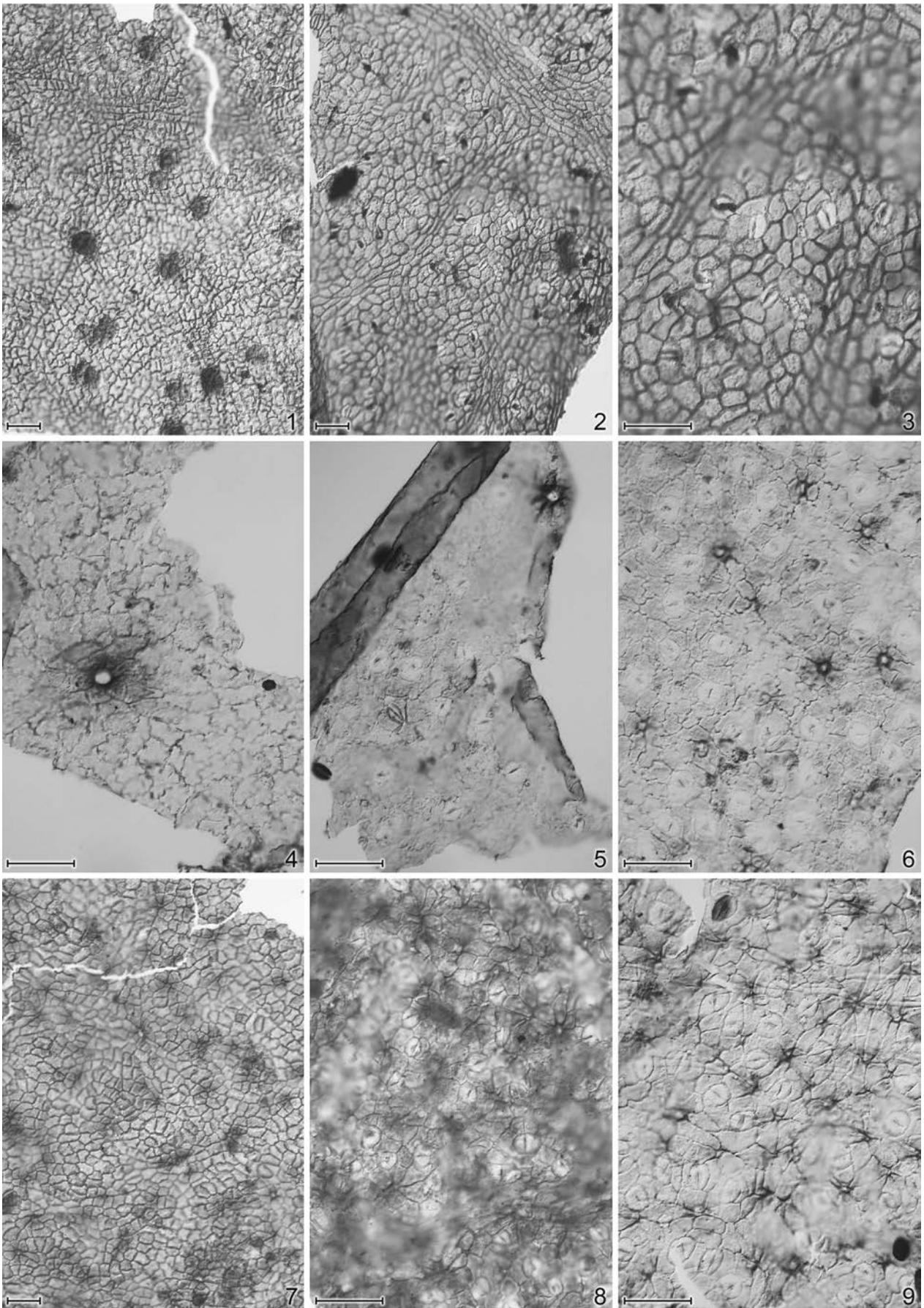
7–8. Probable sun leaf

7. Adaxial cuticle with rather straight anticlines, SMNS P 1952/76-2

8. Abaxial cuticle with trichome bases, SMNS P 1952/76-2

9. Abaxial cuticle of a probable sun leaf with dense trichome bases, SMNS P 1952/472-1

Scale bar: 50  $\mu\text{m}$



## Plate 10

1–3. *Laurus abchasica* (Kolakovskii & Shakryl) Ferguson

1. Adaxial cuticle with ? hypodermis, SMNS P 1953/65-2

## 2–3. Abaxial cuticle

2. SMNS P 1953/65-2

3. SMNS P 1953/75-2

4–9. *Laurophyllum rauenbergense* Kovar-Eder sp. nov.

4. Adaxial cuticle, SMNS P1953/82-1, holotype

5. Abaxial cuticle, non-modified cells somewhat domed, stomata indistinct, SMNS P 1953/82-2, holotype

6. Abaxial cuticle, non-modified cells somewhat domed, stomata indistinct, SMNS P 1952/391-1, paratype

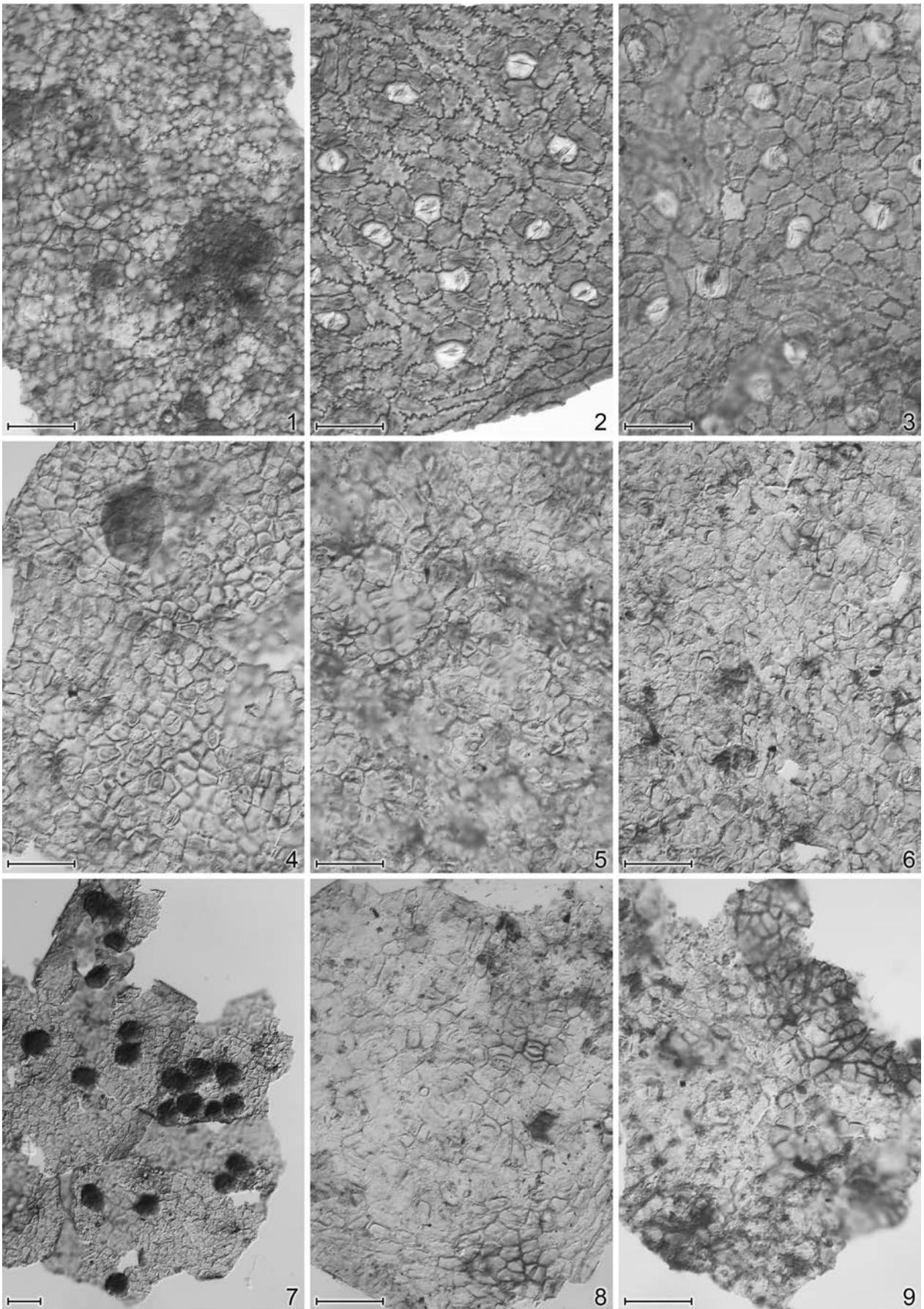
7. Adaxial cuticle with distinct, large oil glands, SMNS P 1952/93-1, paratype

## 8–9. Abaxial cuticle

8. SMNS P 1952/445-2, paratype

9. SMNS P 1953/47-1, paratype

Scale bar: 50  $\mu$ m



## Plate 11

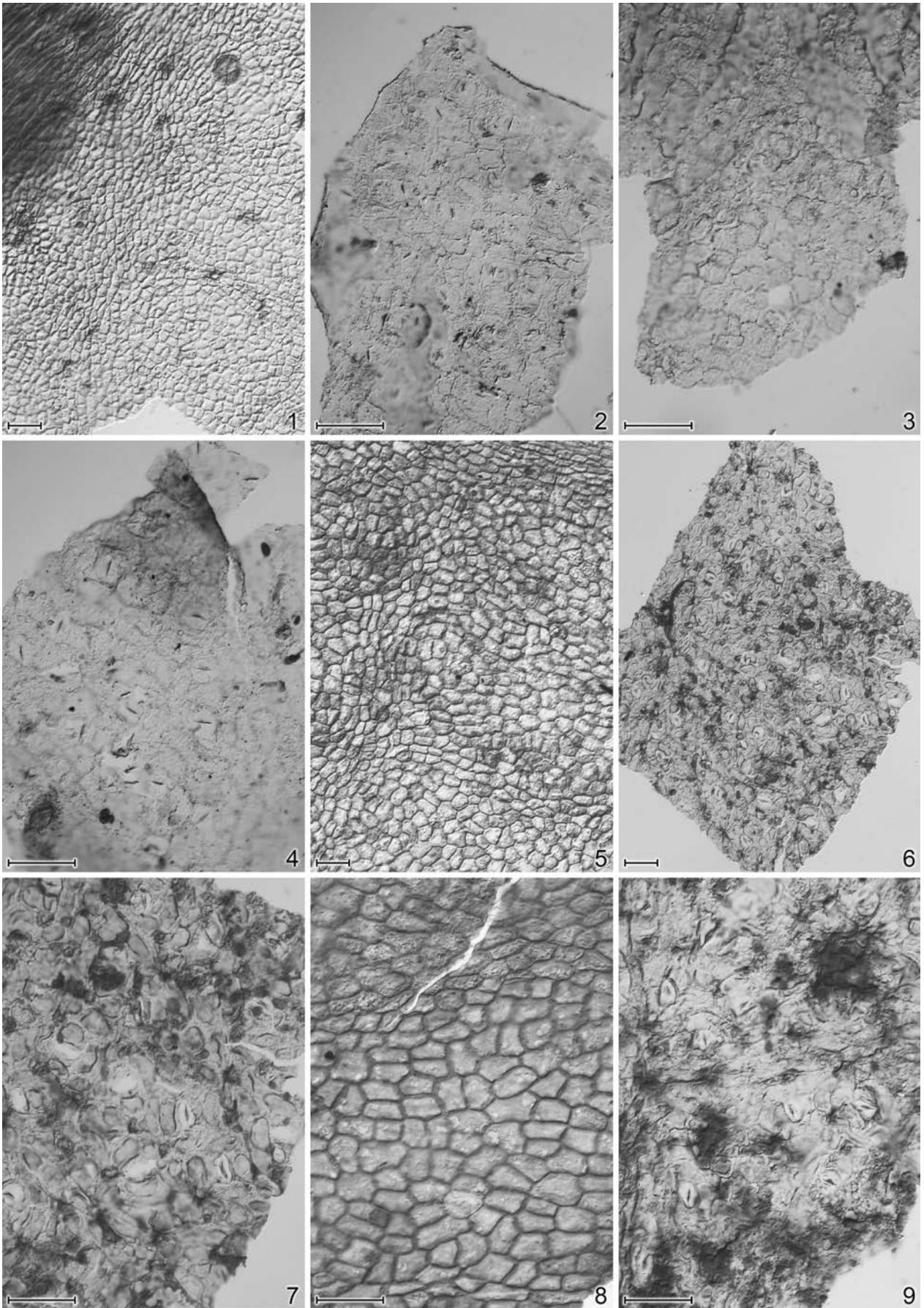
1–4. *Laurophyllum ? rauenbergense* Kovar-Eder sp. nov.

1. Adaxial cuticle with slight striae around trichome base, SMNS P 1952/231-2
2. Abaxial cuticle SMNS P 1952/231-1
3. Adaxial cuticle SMNS P 1953/59-1
4. Abaxial cuticle SMNS P 1953/59-1

5–9. *Laurophyllum kinkelinii* (Engelhardt) Kvaček

5. Adaxial cuticle, SMNS P 1952/184-1
- 6–7. Abaxial cuticle with distinctly domed non-modified cells, SMNS P 1952/184-3
7. Close-up view of 6.
8. Adaxial cuticle, SMNS P 1953/64-1
9. Abaxial cuticle, SMNS P 1953/64-2

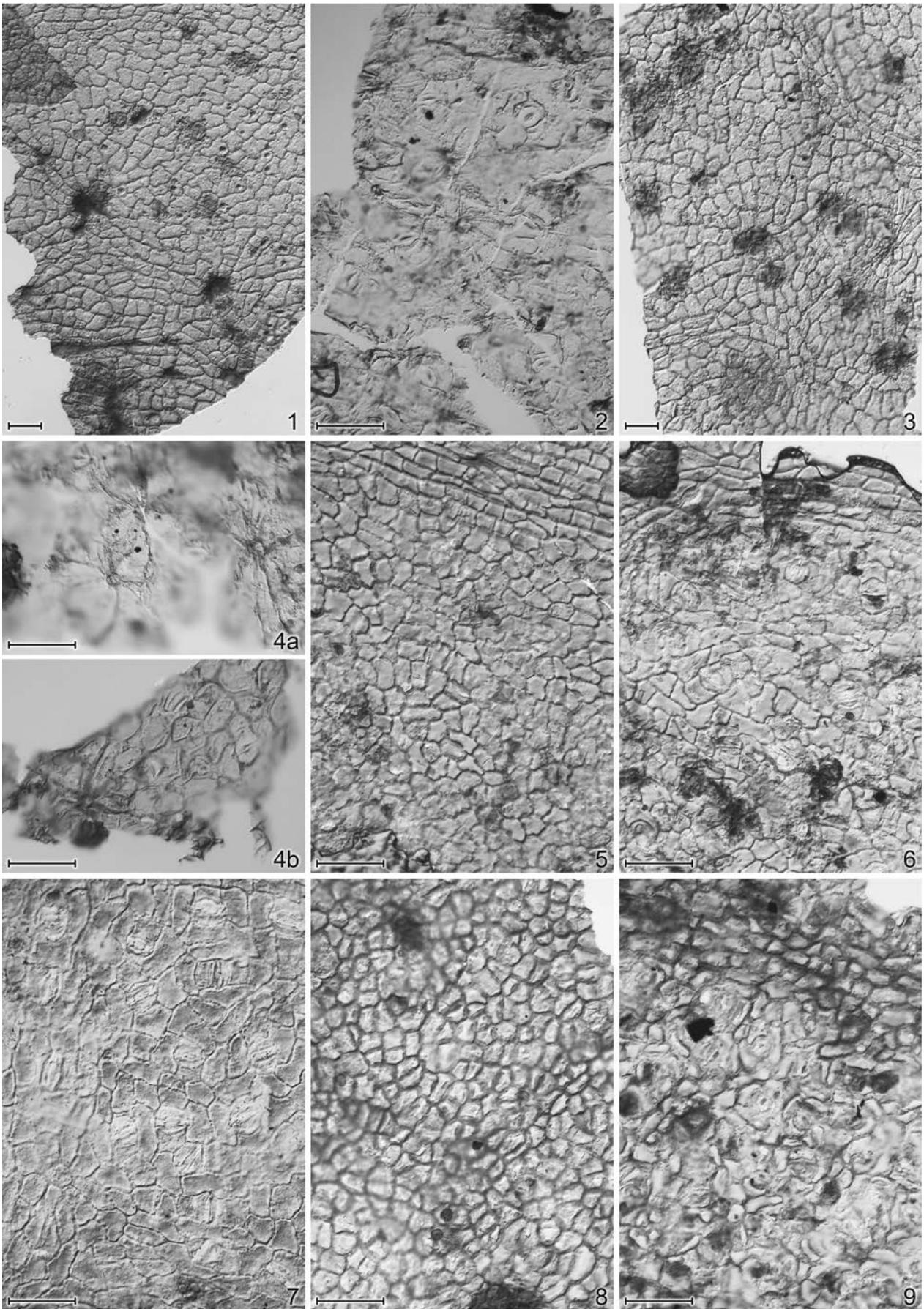
Scale bar: 50  $\mu\text{m}$



## Plate 12

- 1–4. *Laurophyllum* cf. *kinkelinii* (Engelhardt) Kvaček 2004 var. *glabrum* Kvaček
1. Adaxial cuticle, SMNS P 1952/378-1
  2. Abaxial cuticle, trichome bases large with radial striae, SMNS P 1952/378-2
  3. Adaxial cuticle with striae upon veins and trichome base, SMNS P 1953/87-1
  4. Abaxial cuticle
- 4a. Trichome bases, SMNS P 1953/87-1
- 4b. Domed cells and sunken, overlapped stomata, SMNS P 1953/87-2
- 5–7. *Laurophyllum pseudoprinceps* Weyland & Kilpper s.l.
5. Adaxial cuticle, SMNS P 1952/389-2
  6. Abaxial cuticle, SMNS P 1952/389-2
  7. Abaxial cuticle, SMNS P 1953/15A-2
- 8–9. *Laurophyllum* sp. A
8. Adaxial cuticle, SMNS P 1952/336-2
  9. Abaxial cuticle, SMNS P 1952/336-1

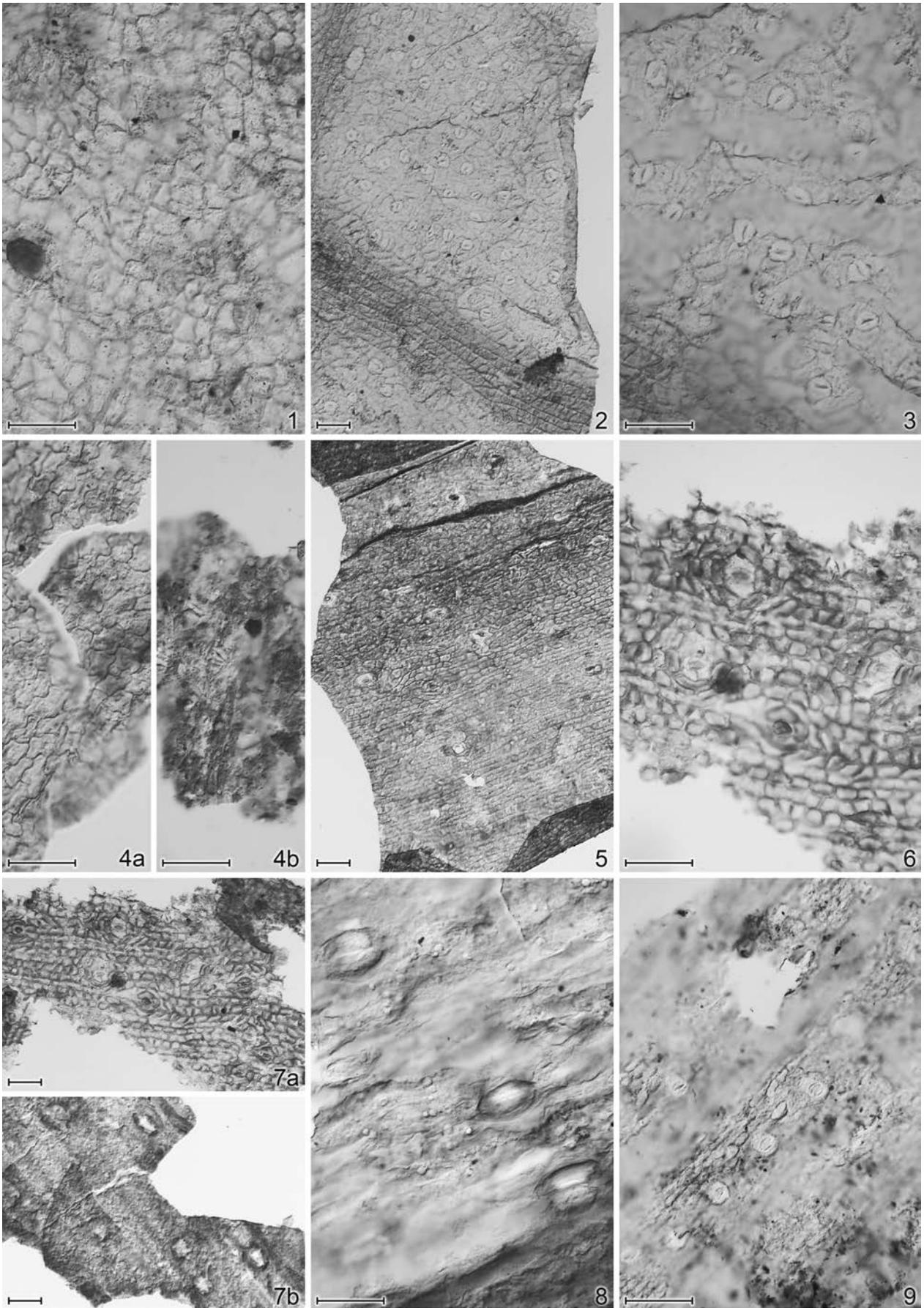
Scale bar: 50  $\mu$ m



## Plate 13

- 1–3. *Laurophyllum* sp. B
  1. Adaxial cuticle with a single oil gland, SMNS P 1952/47-1
  - 2–3. Abaxial cuticle, SMNS P 1952/47-1
    3. Close-up view of 2.
    4. *Laurophyllum* sp. C
- 4a. Adaxial cuticle, SMNS P 1953/81-2
- 4b. Abaxial cuticle, SMNS P 1953/81-2
5. *Palmacites lamanonis* Brongniart, cuticle in stoma-bearing condition, loosely spaced brachyparatetracytic stomatal complexes, 1952/66-1
- 6–7a. ? Calamoideae gen. et sp. indet., cuticle in stoma-bearing condition, paratetracytic to cyclocytic stomatal complexes, NMA 2016-1/1497-1
  6. Close-up view of 7a.
- 7b–8. Areceaceae gen. et sp. indet., cuticle in stoma-bearing condition, NMA 2016-2/1497-1
  8. Close-up view of 7b.
  9. *Phoenicites* sp., Cuticle in stoma-bearing condition, SMNS P 1952/12-1

Scale bar: 50  $\mu$ m

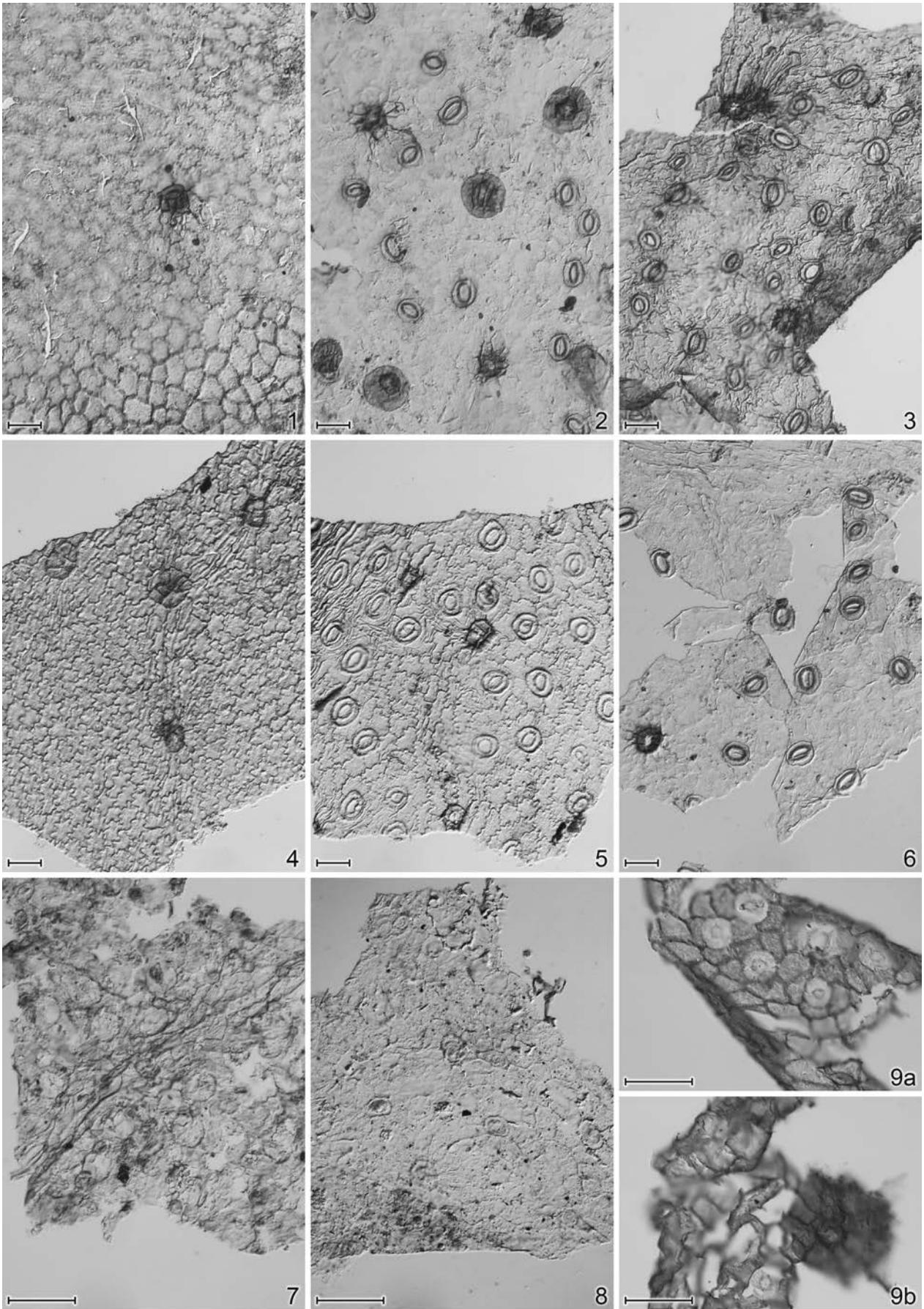


## Plate 14

1–6. *Platanus neptuni* (Ettingshausen) Bůžek, Holý et Kvaček

1. Adaxial cuticle, minutely undulate anticlines and a single gland with at least three base cells, SMNS P 1952/32-1
2. Abaxial cuticle, anticlines vaguely visible, numerous glands, SMNS P1952/32-1
3. Abaxial cuticle, distinct striae to wrinkles, SMNS P 1952/37-1
4. Adaxial cuticle, undulation coarser than in 1., several glands and striation upon veins, SMNS P 1952/465-2
5. Abaxial cuticle, stomata in subparallel position along the margin, SMNS P 1952/465-2
6. Abaxial cuticle, stomatal ledges extremely pronounced but anticlines hardly visible, SMNS P 1953/44-1
7. *Eotrigonobalanus furcinervis* (Rossmässler) Walther & Kvaček forma *haselbachensis* (Kvaček & Walther) Kvaček & Walther in Walther, abaxial cuticle, roundish stomatal complexes and simple trichome bases, SMNS P 1953/60-1
8. Betulaceae vel Ulmaceae gen. et sp. indet., abaxial cuticle, SMNS P 1952/437-1
9. *Myrica* cf. *lignitum* (Unger) Saporta sensu Ettingshausen & Standfest
- 9a. Abaxial cuticle with stomata, SMNS P 1952/361-1
- 9b. Abaxial cuticle with stoma and peltate trichome, SMNS P 1952/361-2

Scale bar: 50 µm



## Plate 15

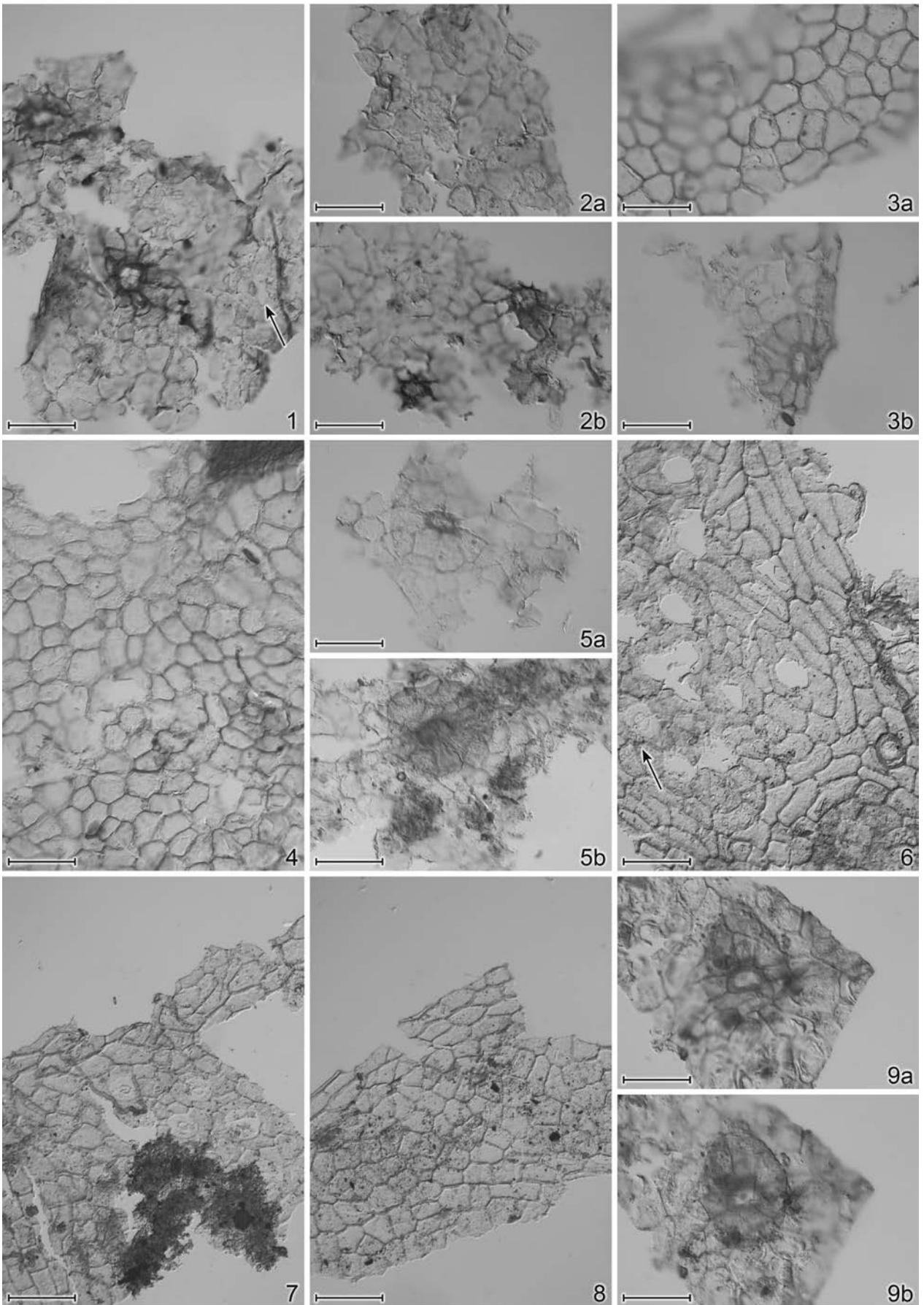
1–2. *Myrica longifolia* Unger

1. Abaxial cuticle, stoma (arrow), four-celled trichome base, SMNS P 1952/50-1
- 2a. ? Adaxial cuticle, SMNS P 1952/186-1
- 2b. Abaxial cuticle, pluricellular trichome bases, SMNS P 1952/186-1

3–9. *Myrica obliquifolia* sp. nov.

- 3a. Adaxial cuticle, SMNS P 1952/85-1, holotype
- 3b. Peltate trichome with oblong, two-celled trichome base, SMNS P 1952/85-1, holotype
4. Adaxial cuticle, SMNS P 1952/232-4, paratype
- 5a–b. Peltate trichomes with oblong, two-celled trichome bases
- 5a. SMNS P 1952/232-5 paratype
- 5b. SMNS P 1952/232-4 paratype
6. Abaxial cuticle, mainly stoma space visible, except for a single one preserved (arrow), SMNS P 1952/238-1, paratype
7. Abaxial cuticle, stomata, SMNS P 1952/255-1, paratype
8. Adaxial cuticle, SMNS P 1952/255-2, paratype
- 9a–b. Peltate trichome focused differently, SMNS P 1953/99-2, paratype
- 9a. Focus on trichome base
- 9b. Focus on peltate trichome

Scale bar: 50 µm



## Plate 16

1–3. *Distylium metzleri* Kovar-Eder sp. nov.

1. Abaxial cuticle, concentric striae upon stomata, parallel wrinkles upon veins and parallel to radial ones around trichome base, SMNS P 1952/43-1, holotype
2. Abaxial cuticle, concentric striae upon stomata, SMNS P 1952/43-2, holotype
3. Adaxial cuticle, SMNS P 1952/43-2, holotype

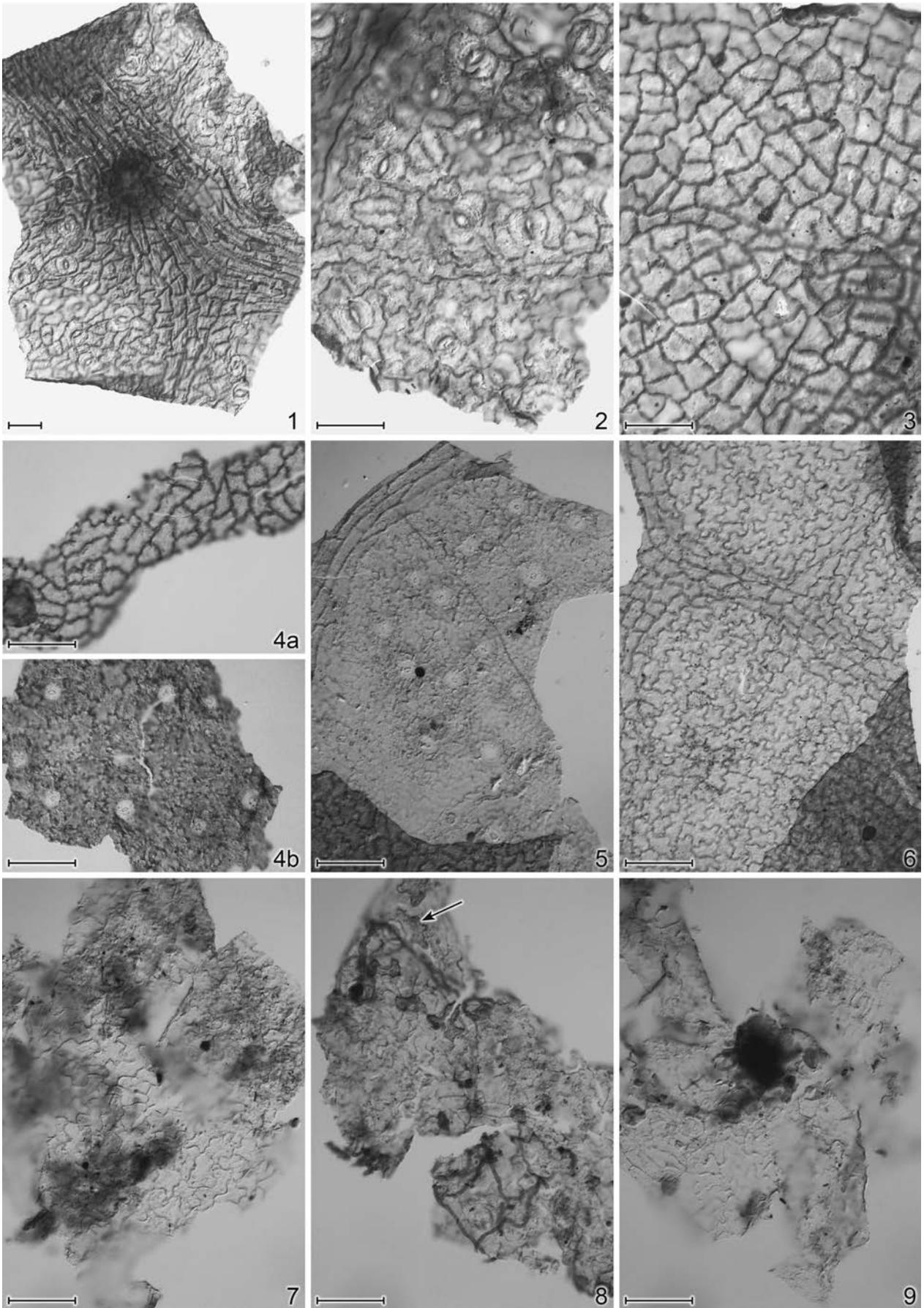
4–6. *Sloanea olmediaefolia* (Unger) Z. Kvaček & Hably

- 4a. Adaxial cuticle, NMA 2006-114/1497-2
- 4b. Abaxial cuticle, stomata roundish, cyclo- to anomocytic, NMA 2006-114/1497-2
5. Abaxial cuticle, stomata roundish, cyclo- to anomocytic, SMNS P 1952/340-1
6. Adaxial cuticle, SMNS P 1952/340-1

7–9. ? *Berchemia altorhenana* Kovar-Eder sp. nov.

7. Adaxial cuticle, zig-zag coarse of anticlines, SMNS P 1953/92-2, holotype
8. Abaxial cuticle, stomata masked by hyphae of fungi (arrow), trichome bases, SMNS P 1953/92-1, holotype
9. Abaxial cuticle, several stomata, SMNS P 1953/92-2, holotype

Scale bar: 50 µm



## Plate 17

1–3. ? *Ternstroemites maritiae* Kovar-Eder sp. nov.

1a. Adaxial cuticle with strongly undulate anticlines, SMNS P 1952/342-1, holotype,

1b. Abaxial cuticle, SMNS P 1952/342-1, holotype

2–3. Abaxial cuticle, SMNS P 1952/342-2, holotype

4–6. *Symplocos deichmuelleri* (Kvaček & Walther) comb. nov.

4. Adaxial cuticle, SMNS P 1952/62-1

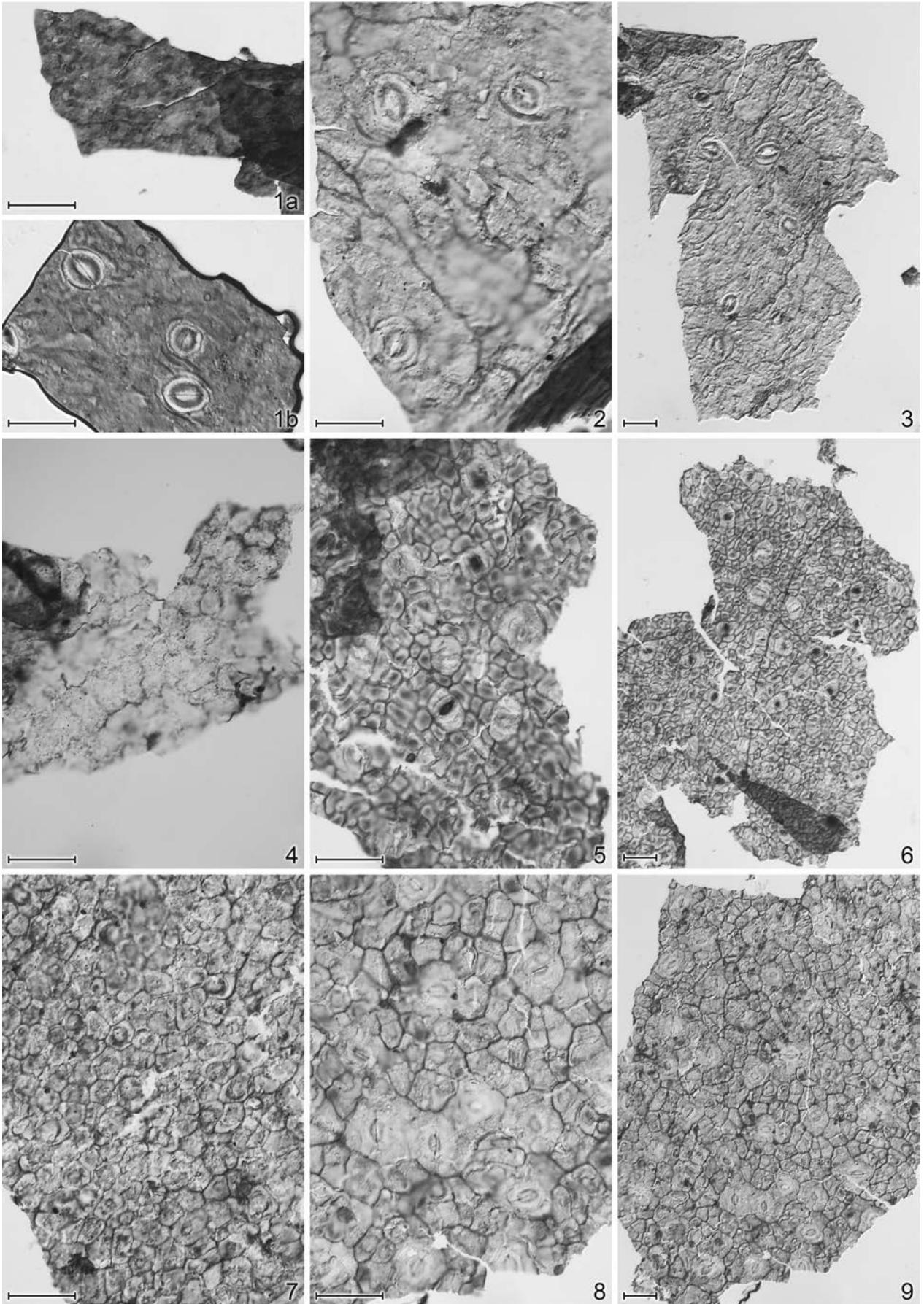
5–6. Abaxial cuticle, SMNS P 1952/65-1

7–9. *Trachelospermum steiningeri* Kvaček

7. Adaxial cuticle with remains of secretory bodies, SMNS P 1952/366-2

8–9. Abaxial cuticle, stomata cyclocytic, remains of secretory bodies, SMNS P 1952/366-2

Scale bar: 50 µm



## Plate 18

1–2. *Trachelospermum steiningeri* Kvaček

1. Adaxial cuticle with numerous, well-preserved secretory bodies, SMNS P 1952/101-2
2. Abaxial cuticle, stomata (arrows), secretory bodies, SMNS P 1952/101-2

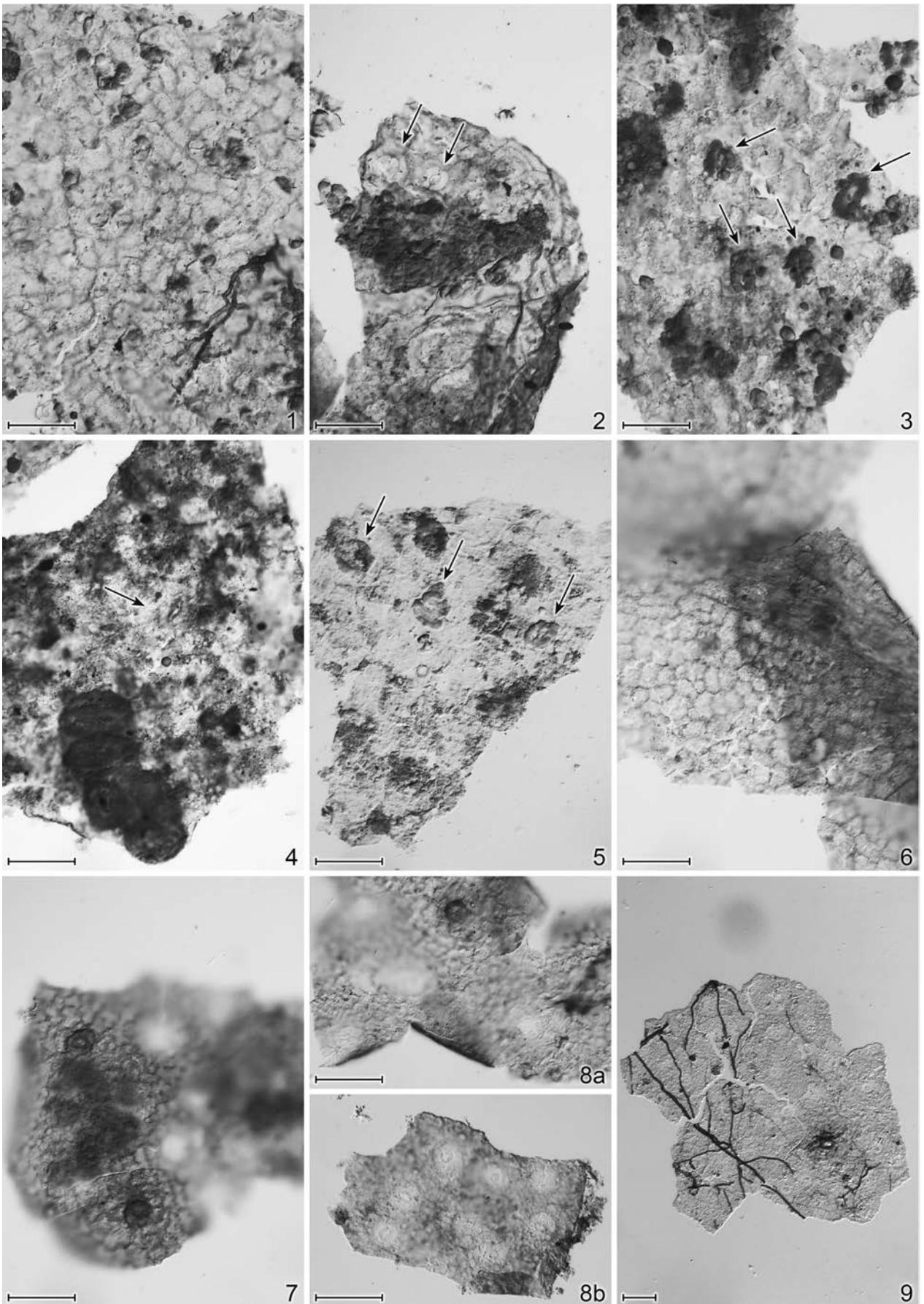
3–5. *Trachelospermum kelleri* Kovar-Eder sp. nov.

3. Abaxial cuticle, secretory bodies dense, masking the stomata (arrows), NMA 2006-121/1497-1, holotype
4. Abaxial cuticle, a single stoma and its aperture visible, NMA 2006-121/1497-1, holotype
5. Abaxial cuticle, secretory bodies masking the stomata (arrows), SMNS P 1953/101-3, paratype

6–9. *Oleinites altorhenana* Kovar-Eder sp. nov.

6. Adaxial cuticle, SMNS P 1952/191-2, holotype
7. Abaxial cuticle, trichome bases, SMNS P 1952/191-2, holotype
- 8a. Abaxial cuticle, trichome base and small non-modified epidermal cells, SMNS P 1952/191-2, holotype
- 8b. Abaxial cuticle, stomata, SMNS P 1952/191-2, holotype
9. Abaxial cuticle, stomata and a single trichome base, SMNS P 1952/388-2, paratype

Scale bar: 50  $\mu$ m



## Plate 19

1–5a. *Oleinites rauenbergensis* Kovar-Eder sp. nov.

1. Adaxial cuticle, SMNS P 1952/380-2, holotype

2a. Probable abaxial cuticle, a prominent trichome base with small peltate head, SMNS P 1952/380-2, holotype

2b. Abaxial cuticle, stomata, SMNS P 1952/380-2, holotype

3a–c. Small fragments of abaxial cuticle with single stomata

3a–b. SMNS P 1952/380-2, holotype

3c. SMNS P 1952/402-2, paratype

4. Adaxial cuticle, SMNS P 1952/402-2, paratype

5a. Abaxial cuticle, SMNS P 1952/402-1, paratype

5b–6. ? *Oleinites rauenbergensis* Kovar-Eder sp. nov.

5b. Cuticle fragment with trichome bases, SMNS P 1952/6-1

6. Abaxial cuticle, SMNS P 1952/6-1

7–9. *Dicotylophyllum badense* Kovar-Eder sp. nov.

7. Adaxial cuticle, SMNS P 1952/200-2, holotype

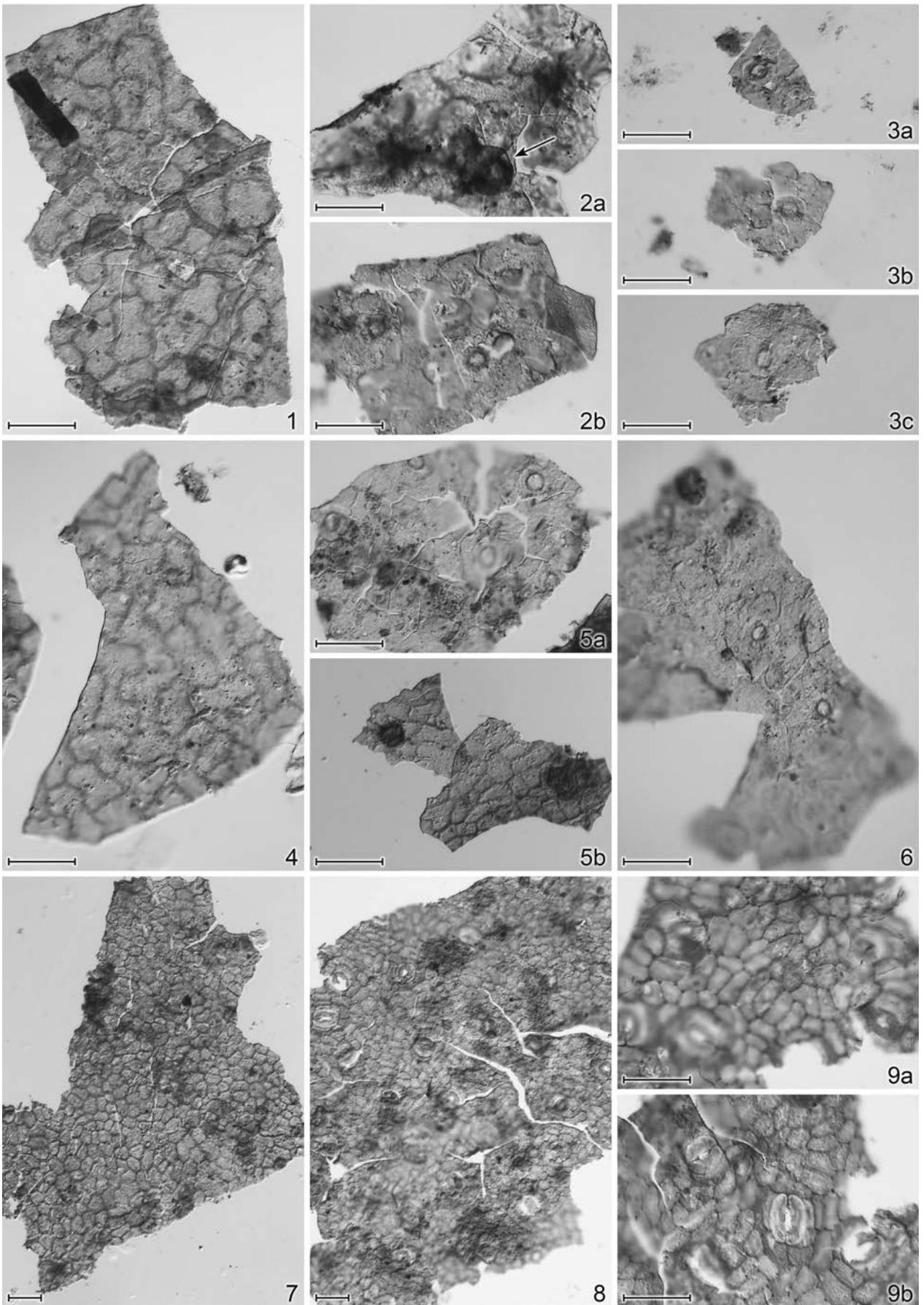
8. Abaxial cuticle, SMNS P 1952/200-3, holotype

9a–b. Abaxial cuticle, stomata

9a. SMNS P 1952/200-2, holotype

9b. SMNS P 1952/200-3, holotype

Scale bar: 50  $\mu\text{m}$



## Plate 20

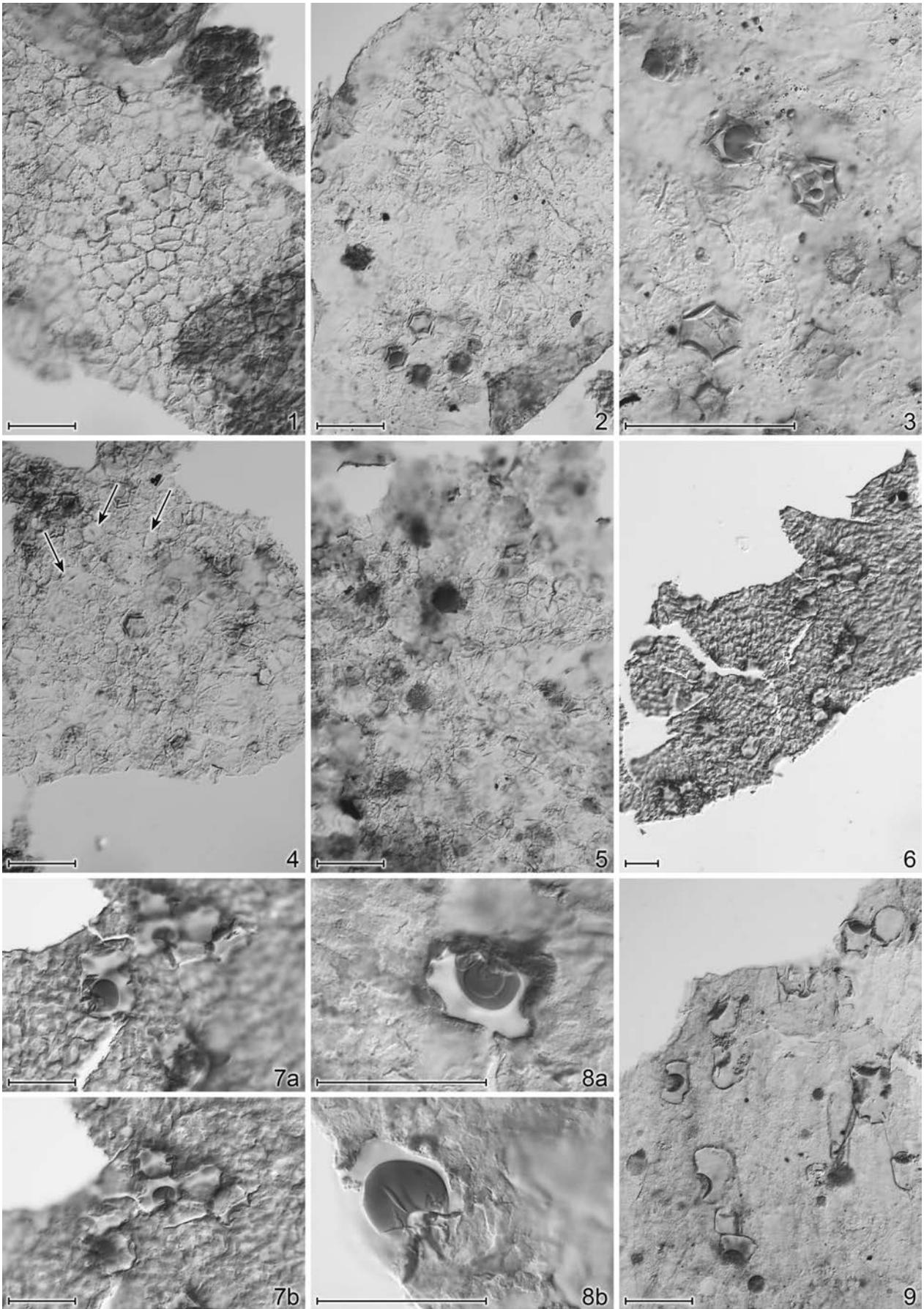
1–5. *Dicotylophyllum vesiculaeferens* Kovar-Eder sp. nov.

1. Adaxial cuticle, SMNS P 1952/310-1, holotype
2. Abaxial cuticle with a group of penta- to hexagonal pouches, some still with secretory content, SMNS P 1952/310-1, holotype
3. Close-up view showing balloon-shaped secretory structures in pouches and empty pouches each with a plurilet central mark (arrow), SMNS P 1952/310-1, holotype
4. Abaxial surface, ? stomata (arrows) and single pouches, SMNS P 1952/310-1, holotype
5. ? Abaxial cuticle with a filled pouch, SMNS P 1952/310-2, holotype

6–9. *Cladites vesiculaeferens* Kovar-Eder sp. nov.

6. Cuticle of the axis, cells arranged in rows and pouches, SMNS P 1952/416-1, holotype
- 7a–b. and 8a–b. Pouches in different close-up views with adherent and embedded balloon-shaped secretory bodies, SMNS P 1952/416-1, holotype
9. Cuticle from a more proximal part of the same axis, cuticle more delicate, cell arrangement not visible, pouches in different stages of development, SMNS P 1952/416-2, holotype

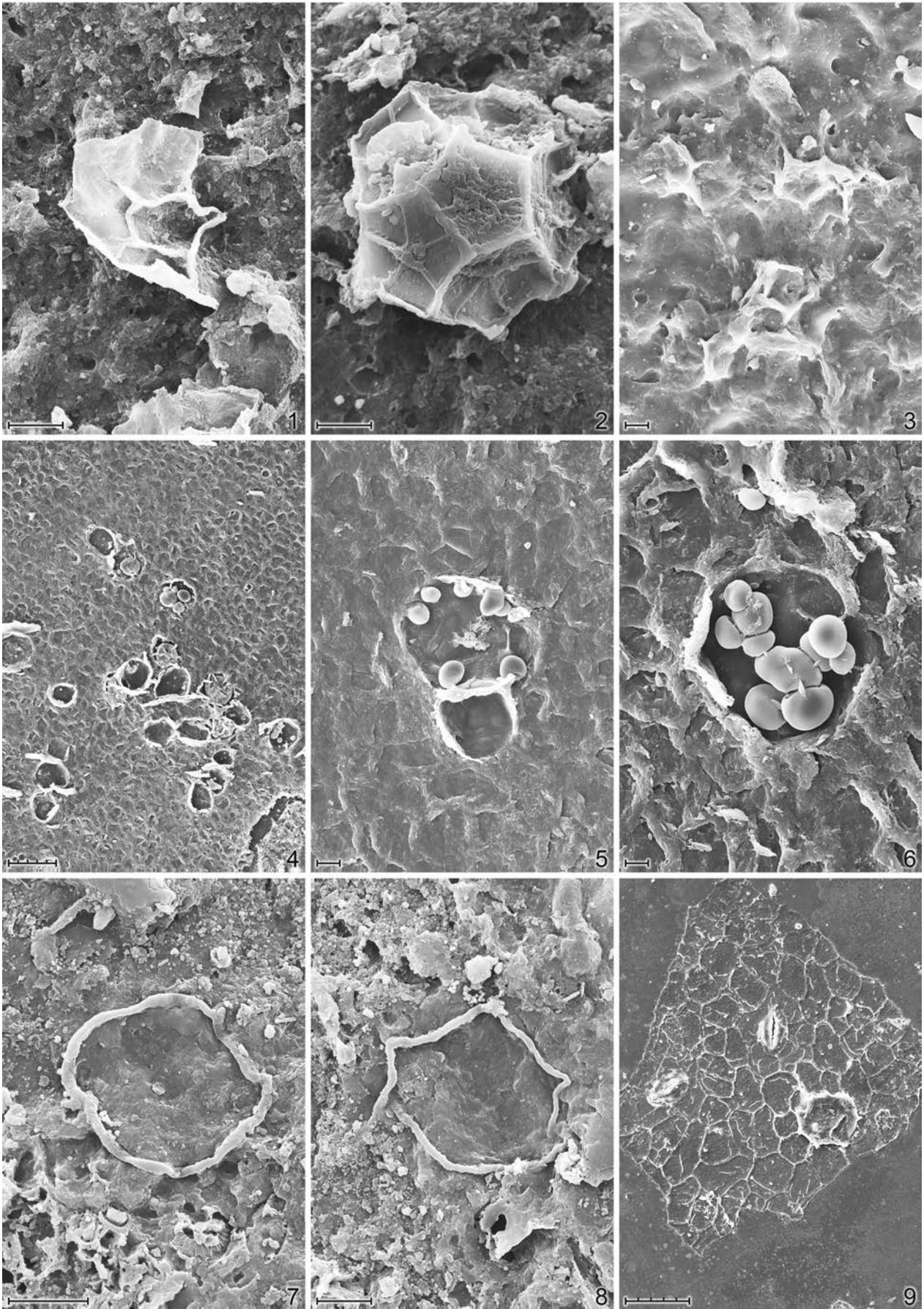
Scale bar: 50  $\mu\text{m}$



## Plate 21

- 1–3. *Dicotylophyllum vesiculaeferens* Kovar-Eder sp. nov., SEM view of SMNS P 1952/310, holotype
- 1–2. External view of secreting structure
3. Internal view of secreting structure
- 4–8. *Cladites vesiculaeferens* Kovar-Eder sp. nov.
- 4–6. Internal view, partly clustered secreting structures, i.e. pouches partly with still adherent vesicles, SEM view of SMNS P 1952/416, holotype
4. scale bar 50  $\mu\text{m}$
6. vesicles appear interconnected
- 7, 8. External view, SMNS P 1952/104
9. *Dicotylophyllum ziegleri* Kovar-Eder sp. nov., SEM view of abaxial cuticle, internal side, two cyclocytic stomata and a single gland, SMNS P 1953/86, holotype, scale bar 50  $\mu\text{m}$

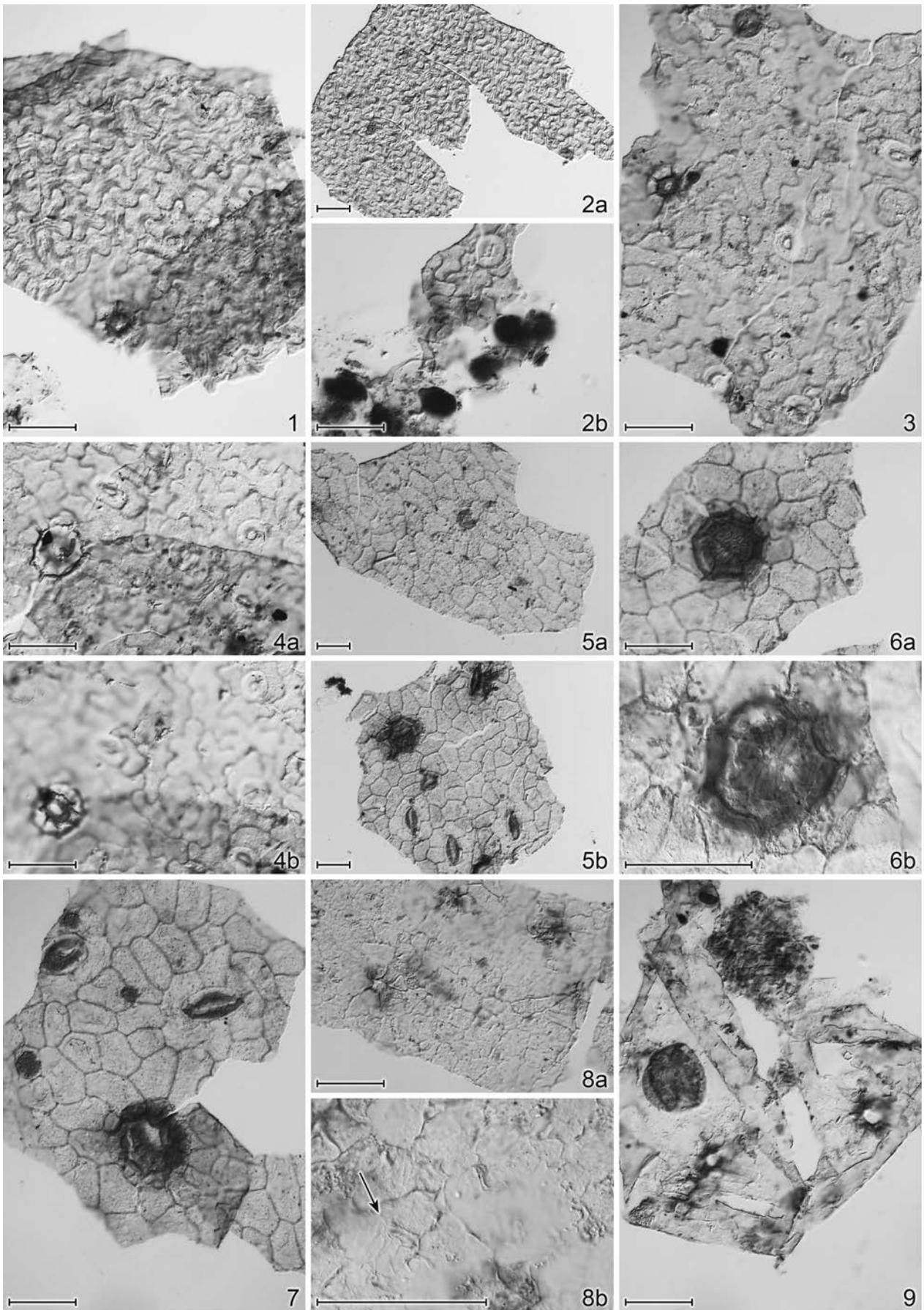
If not noted otherwise, scale bar: 5  $\mu\text{m}$



## Plate 22

- 1–4. *Dicotylophyllum oechsleri* Kovar-Eder sp. nov.
1. Adaxial cuticle, strongly sinuous anticlines, distinct striation, base of a glandular trichome SMNS P 1952/454-1, holotype
  - 2a. Adaxial cuticle, SMNS P 1952/454-2, holotype
- 2b–4b. Abaxial cuticle, SMNS P 1952/454-1, holotype
- 2b. Stoma and mesophyll remains
  3. Stomata and prominent trichome base of a disc-shaped or globular head
- 4a–b. Trichome base with depression of the head
- 4a. Focus on the marginal ridge of the head
  - 4b. Same position as 4a. but focus on the collar-like margin of the trichome base
- 5–7. *Dicotylophyllum ziegleri* Kovar-Eder sp. nov.
- 5a. Adaxial cuticle, SMNS P1953/86-1, holotype
  - 5b. Abaxial cuticle, subparallel stoma orientation, stomata cyclo- to actinocytic, somewhat grouped, SMNS P 1953/86-2, holotype
- 6a–b. Epidermal glands marginally overlapped by the surrounding, marginally strongly thickened cells
- 6a. SMNS P 1953/86-2, holotype
  - 6b. SMNS 1953/86-1, holotype
7. Abaxial cuticle with stomata and gland, SMNS P 1953/86-2, holotype
- 8–9. *Dicotylophyllum* sp.
- 8a–b. Abaxial cuticle, SMNS P 1952/400-1
- 8a. Cell outlines more or less vaguely visible, ? stomata, trichome bases
  - 8b. A single ? stoma (arrow)
9. Adaxial cuticle with large trichome bases, SMNS P 1952/400-1

Scale bar: 50 µm

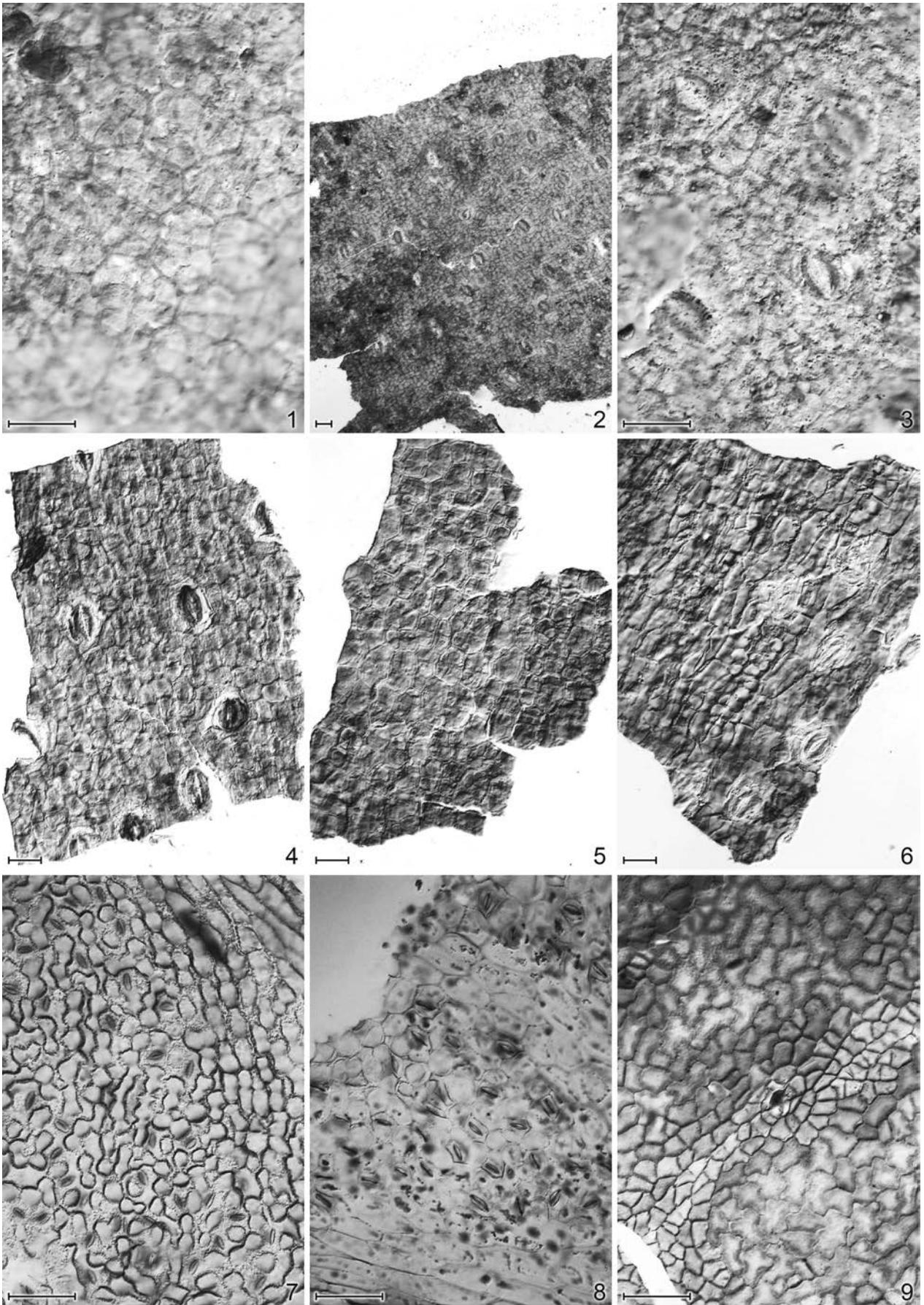


## Plate 23

1–6. *Viscophyllum hendriksiae* Kovar-Eder sp. nov.

1. Adaxial cuticle, SMNS P 1953/70-1, holotype
2. Abaxial cuticle, cells more or less arranged in rows, subparallel stoma orientation, SMNS P 1953/70-1, holotype
3. Abaxial cuticle, close-up, SMNS P 1953/70-1, holotype
4. Abaxial cuticle, SMNS P 1952/11-1, paratype
5. Adaxial cuticle, ? hypodermis, SMNS P 1953/71-2, paratype
6. Abaxial cuticle, SMNS P 1953/71-2, paratype
7. *Berchemia philippinensis* Vid., abaxial cuticle, non-modified cells domed, partly overlapping stomata, surface granular, SMNS 2015/18-1
8. *Berchemia lineata* (L.) DC., abaxial cuticle, stomata partly overlapped by non-modified cells, SMNS 2015/16-1
9. *Berchemia affinis* Hassk., adaxial cuticle, anticlines of non-modified cells somewhat zig-zag undulate, trichome base with intensively staining foot, SMNS 2015/7-1

Scale bar: 50  $\mu$ m



**Appendix 1.** Cuticular features of ? *Berchemia altorhenana* Kovar-Eder sp. nov. compared to modern species of *Berchemia*

<i>Berchemia</i> species	Abaxial surface				
	stomata	stoma length (average) × width (average), aperture length (AL), average in brackets, [µm]	anticlines of non-modified epidermal cells	surface of non-modified epidermal cells	size of non-modified epidermal cells, [µm]
<i>B. altorhenana</i> Kovar-Eder sp. nov.	slightly sunken, overlapped by surrounding cuticle	17–25 (21) × 10–21 (15), AL = 10–17	moderately undulate	not domed	24–38 (35)
<i>B. affinis</i> Hassk.	not sunken	9–13 (11) × 6–11 (9), AL = 4–6 (5)	somewhat shallowly undulate	not domed	10–15 (12)
<i>B. berchemiaefolia</i> Koidz.	not to somewhat sunken	13–15 × 7–10, AL = 8–14 (10)	not reproduced on cuticle, straight-bent	somewhat domed	not measurable
<i>B. chanetii</i> Lév.	not sunken	12–18 (14) × 9–12 (11), AL = 6–11 (9)	hardly reproduced on cuticle, straight-bent	not domed	not measurable
<i>B. edgeworthii</i> Law.	not sunken	AL = 8–11 (9)	hardly reproduced on cuticle, bent	somewhat domed	not measurable
<i>B. floribunda</i> (Wall.) Brongn.	not sunken, orientation partly subparallel	AL = 10–14 (13)	delicate, straight	not domed	23–45 (36)
<i>B. flavescens</i> (Wall.) Brongn.	sunken	AL = 13–20 (15)	hardly reproduced on cuticle	domed	not measurable
<i>B. fournieri</i> Pancher	not sunken	15–19 (16) × 11–14 (13), AL = 8–11 (9)	distinct, slender, straight to somewhat wavy	not domed	13–26 (20)
<i>B. giraldiana</i> Schn.	sunken	AL = 9–12 (11)	not reproduced on cuticle	strongly domed, papillae-like	not measurable
<i>B. kulingensis</i> Schneid.	sunken	AL = 8–11 (10)	not reproduced on cuticle	strongly domed	not measurable
<i>B. lineata</i> (L.) CD.	sunken, orientation partly subparallel	13–18 (15) × ??, AL = 8–13 (10)	delicate, straight	domed	16–23 (20)
<i>B. longeracemosa</i> Okuyama	not sunken, partly subparallel	14–20 (16) × ??, AL=8–12 (10)	hardly reproduced on cuticle, straight-bent	slightly domed	not measurable
<i>B. philippinensis</i> Vid.	distinctly sunken	AL = 9–12 (10)	not reproduced on cuticle	strongly domed, papillae-like	not measurable
<i>B. racemosa</i> S. & Z.	distinctly sunken	13–17 (15) × 12–13 (12), AL = 9–11 (10)	delicate, straight to bent, only reproduced along veins	strongly domed, papillae-like	not measurable
<i>B. sinica</i> Schn.	not sunken, orientation partly subparallel	AL= 9–13 (11)	not reproduced on cuticle	slightly domed	not measurable
<i>B. yunnanensis</i> Franch.	distinctly sunken	AL = 7–11 (9)	not reproduced on cuticle	strongly domed, papillae-like	17–27 (22)

## Appendix 1. Continued

		Adaxial cuticle				
indumentum	idiocuticular structure	anticlines of non-modified epidermal cells	surface of non-modified epidermal cells	size of non-modified epidermal cells, [ $\mu\text{m}$ ]	indumentum	idio-cuticular structure
trichome bases scattered, not dense	smooth	moderately zig-zag undulate	not domed	24–38 (35)	scattered trichome bases, dark-staining centre, sometimes ring of small encircling cells	smooth
absent	smooth	slender, smooth, moderately a bit zig-zag undulate	not domed	15–31 (22)	scattered trichome bases, dark-staining center, ring of small encircling cells	smooth
trichomes rare	granulate	hardly reproduced on cuticle, straight-bent	slightly domed	not measurable	trichome bases rare with ring of short girdling cells	granulate
glabrous	somewhat granulate	hardly reproduced on the cuticle, straight-bent	not domed	not measurable	glabrous	granulate
glabrous	granulate	distinct, smooth, straight	not domed	18–39 (27)	glabrous	granulate
glabrous	finely granulate	very thick, straight, continuous, resolving into pits to vaguely visible	not domed	27–51 (34)	largely glabrous	roughly granulate
glabrous	finely granulate	distinct, straight, smooth	not domed	29–44 (36)	glabrous	finely granulate, additionally scattered folds
glabrous	rather smooth, occasionally delicate folding	distinct, slender, straight, smooth but pitted on the inner side	not domed	16–36 (24)	glabrous	somewhat finely granulate
trichomes abundant	granulate	hardly reproduced on cuticle, straight	not domed	not measurable	glabrous	granulate
glabrous	granulate	faintly reproduced on cuticle, straight	not domed	42–60 (53)	glabrous	granulate
glabrous	smooth	vaguely visible, straight, slender	not domed	26–47 (33)	glabrous	granulate to rugulate
glabrous	granulate	vaguely visible, straight, slender	slightly domed	32–43 (37)	glabrous	granulate
glabrous	strongly granulate	thick, straight, smooth	not domed	13–20 (17)	glabrous	granulate
glabrous	strongly granulate	thick, straight, smooth, desintegrating into pits	not domed	20–36 (30)	glabrous	granulate
glabrous	granulate	thick, straight, smooth	not domed	19–33 (26)	glabrous	somewhat granulate
trichomes abundant	smooth	thick, straight, smooth, desintegrating into pits to hardly traceable	not domed	17–27 (22)	glabrous	granulate

**Appendix 2.** Score sheet of the IPR vegetation analysis (after Kovar-Eder & Kvaček 2008, Teodoridis et al. 2011a)

Taxon	Zonal									Azonal			Problematic taxa/ unaccounted	Control
	CONIF	BLD	BLE	SCL	LEG	arboreal palm	arboreal fern	d-herb	m-herb	azonal woody	azonal non-woody	aquatic		
<i>Cystoseirites communis</i>												1.0		1.0
<i>Thallites multifidus</i>												1.0		1.0
<i>Laminarites latus</i>												1.0		1.0
<i>Lygodium kaulfussii</i>									0.5		0.5			1.0
<i>Filicopsida</i> sp.									0.5		0.5			1.0
<i>Ceratozamia floersheimensis</i>			1.0											1.0
<i>Doliosobus taxiformis</i> ? <i>taxiformis</i>	0.5									0.5				1.0
<i>Sequoia abietina</i>	0.5									0.5				1.0
<i>Taxodium</i> sp.										1.0				1.0
<i>Tetraclinis salicornioides</i>	1.0													1.0
<i>Pinus (Strobilus)</i> sp. 1	0.5									0.5				1.0
<i>Pinus (Strobilus)</i> sp. 2	0.5									0.5				1.0
<i>Pinus</i> sp. 3	0.5									0.5				1.0
<i>Pinus</i> sp. 4	0.5									0.5				1.0
<i>Pinus</i> sp. 5	0.5									0.5				1.0
<i>Pinus</i> sp. 6	0.5									0.5				1.0
<i>Pinus (Pinus)</i> cf. <i>thomasiana</i>										1.0				1.0
<i>Pinus engelhardtii</i>	0.5									0.5				1.0
<i>Actinodaphne pseudogermari</i>			1.0											1.0
<i>Daphnogene cinnamomifolia</i>			0.5							0.5				1.0
<i>Laurus abchasicus</i>			1.0											1.0
<i>Laurophyllum kinkelinii</i> inkl. <i>L. kinkelinii glabrum</i>			1.0											1.0
<i>Laurophyllum pseudoprinceps</i>			0.5							0.5				1.0
<i>Laurophyllum rauenbergense</i>			0.5	0.5										1.0
<i>Laurophyllum</i> sp. A			1.0											1.0
<i>Laurophyllum</i> sp. B			1.0											1.0
<i>Laurophyllum</i> sp. C			1.0											1.0
<i>Palmacites lamanonis</i>						0.5				0.5				1.0
<i>Sabalites major</i>						0.5				0.5				1.0
<i>Phoenicites</i> sp.						0.5				0.5				1.0
? Calamoideae gen. et sp. indet.						0.5				0.5				1.0
Arecaceae gen. et sp. indet.						0.5				0.5				1.0
<i>Platanus neptuni</i>										1.0				1.0
? <i>Buxus egeriana</i>			0.5		0.5									1.0
<i>Eotrigonobalanus furcinervis</i> f. <i>haselbachensis</i>			1.0											1.0
<i>Betula dryadum</i>		1.0												1.0
Betulaceae vel Ulmaceae gen. et sp. indet.		1.0												1.0
<i>Comptonia difformis</i>		0.5	0.5											1.0
<i>Myrica</i> cf. <i>lignitum</i>		0.3	0.3							0.3				1.0
<i>Myrica longifolia</i>			1.0											1.0
<i>Myrica obliquifolia</i>		0.3	0.3							0.3				1.0
<i>Carya fragiliformis</i>		0.5								0.5				1.0
<i>Carya quadrangula</i>		0.5								0.5				1.0
<i>Engelhardia orsbergensis</i> / <i>E. macroptera</i>		0.3	0.3							0.3				1.0
? <i>Berchemia altorhenana</i>		0.5	0.5											1.0
? <i>Leguminocarpon</i> sp.					1.0									1.0
<i>Sloanea artocarpites</i>		0.5	0.5											1.0
<i>Sloanea olmediaefolia</i>		0.5	0.5											1.0
<i>Populus germanica</i>		0.5								0.5				1.0

## Appendix 2. Continued

Taxon	Zonal									Azonal			Problematic taxa/ unaccounted	Control
	CONIF	BLD	BLE	SCL	LEG	arboreal palm	arboreal fern	d-herb	m-herb	azonal woody	azonal non-woody	aquatic		
<i>Craigia brononii</i>		0.5								0.5				1.0
<i>Distylium metzleri</i>		0.5	0.5											1.0
? <i>Viscophyllum hendriksiae</i>			1.0											1.0
<i>Hydrangea microcalyx</i>		1.0												1.0
? <i>Ternstroemites maritiae</i>			1.0											1.0
<i>Symplocos deichmuelleri</i>			1.0											1.0
<i>Trachelospermum kelleri</i>			0.5	0.5										1.0
<i>Trachelospermum steiningeri</i>			0.5	0.5										1.0
<i>Oleinites altorhenana</i>			1.0											1.0
<i>Oleinites rauenbergensis</i>			0.5	0.5										1.0
<i>Pungiphyllum cruciatum</i>			0.5	0.5										1.0
<i>Dicotylophyllum badense</i>			0.5	0.5										1.0
<i>Dicotylophyllum oechsleri</i>			0.5	0.5										1.0
<i>Dicotylophyllum vesiculaeferens</i>			0.5	0.5										1.0
<i>Dicotylophyllum ziegleri</i>			0.5	0.5										1.0
<i>Dicotylophyllum</i> sp.		0.3	0.3	0.3										1.0
<i>Cladites vesiculaeferens</i>													1.0	1.0
Winged fruit or seed incertae sedis													1.0	1.0
Spiny branch													1.0	1.0
sum of taxa	5.5	8.8	22.8	4.8	1.5	2.5	0.0	0.0	1.0	14.0	1.0	3.0	3.0	68.0
sum of zonal taxa														47.0
percent of all zonal taxa	11.7	18.8	48.6	10.3	3.2	5.3	0.0	0.0	2.1					100.0

**Appendix 3.** Climate data from the distribution region of the evergreen sclerophyllous broad-leaved forest sensu Wang (1961) as well as *Platanus kerrii*, *Sloanea*, and *Ceratotamia* today. MAT – mean annual temperature, CMMT – coldest month mean temperature, WMMT – warmest month mean temperature, MAP – mean annual precipitation, WMMP – wettest month mean precipitation, DMMP – driest month mean precipitation. Climate data derived from <http://de.climate-data.org>

Climate station	Longitude	Latitude	Altitude [m]	MAT [°C]	Warmest month	WMMT [°C]	Coldest month	CMMT [°C]	MAP [mm]	Wettest month	WMMP [mm]	Driest month	DMMP [mm]	Climate type sensu Köppen
<b>Thailand</b>														
1 Nakhon Sawan	100°08'E	15°42'N	29	28.2	April	31.3	Dec	24.7	1143	Sept	249	Dec	4	Aw
2 Chiang Rai	99°50'E	19°55'N	397	24.6	May	27.6	Jan	19.5	1737	Aug	434	Feb	8	Aw
<b>Vietnam</b>														
3 Da Nang, Vietnam	108°21'E	16°04'N	10	25.7	June	29.2	Jan	21.4	2075	Oct	553	March	30	Am
4 Hanoi, Vietnam	105°51'E	21°02'N	21	23.8	June	29.4	Jan	16.6	1684	Aug	338	Jan	16	Cwa
5 Lào Cai, Vietnam	103°57'E	22°29'N	112	23.8	June	28.3	Jan	17.1	1735	Aug	330	Jan	18	Cwa
<b>China</b>														
6 Haikou, Hainan	110°15'E	20°00'N	8	24.2	July	28.9	Jan	17.5	1581	Sept	264	Jan	25	Cwa
7 Chongzuo, Guangxi	107°22'E	22°25'N	106	22.8	July	29.0	Jan	14.5	1518	June	270	Dec	30	Cfa
8 Nanning, Guangxi	108°13'E	22°38'N	81	22.5	July	29.1	Jan	13.7	1363	June	228	Dec	30	Cfa
9 Guigang, Guangxi	109°37'E	23°06'N	52	21.9	July	29.0	Jan	12.9	1469	May	258	Nov	38	Cfa
10 Guangzhou, Guangdong	113°29'E	23°13'N	18	22.2	July	28.8	Jan	13.9	1720	June	287	Dec	32	Cfa
11 Shantou, Guangdong	116°41'E	23°24'N	15	21.7	July	28.3	Feb	14.2	1527	June	278	Dec	31	Cfa
12 Kunming, Yunnan	102°41'E	25°04'N	1911	15.2	July	20.3	Jan	8.4	999	July	209	Jan	12	Cwb
13 Guilin, Guangxi	110°17'E	25°16'N	155	19.5	July	28.7	Jan	9.0	1775	May	347	Dec	48	Cfa
14 Ganzhou, Jiangxi	114°56'E	25°50'N	120	19.8	July	29.8	Jan	8.4	1467	June	232	Dec	39	Cfa
<b>Mexico</b>														
15 Guanajuato, Gto	101°17'W	21°00'N	2060	17.6	May	20.8	Jan	13.9	697	July	145	Feb	7	Cwb
16 Veracruz	96°08'W	19°09'N	8	25.4	June	28.1	Jan	21.7	1516	July	360	Feb	13	Aw
<b>Guatemala</b>														
17 Aguacatan	91°18'W	15°20'N	3093	10.2	May	11.2	Jan	8.6	1457	Sept	258	Feb	19	Cwb
18 Puerta Parada	90°27'W	14°33'N	1846	17.2	April	18.4	Jan	15.7	1529	June	315	Feb	5	Cwb
20 San Raymundo	90°36'W	14°46'N	1578	18.6	May	19.8	Jan	17.0	1578	June	225	Feb	2	Cwb
19 Olopa	89°20'W	14°41'N	1325	19.9	April	21.7	Dec	17.7	1526	June	284	Jan	28	Cwb