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A Late Miocene (Pannonian) flora from Hinterschlagen, Hausruck lignite area, Upper Austria

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ABSTRACT. A fossil flora is described from the opencast mine Heissler near Hinterschlagen in the Hausruck lignite area (Upper Austria, Late Miocene, Pannonian). The plant remains derive from the top of a clayey seam parting and indicate (shallow) aquatic habitats and species-poor, swampy floodplain forests. *Salix hausruckensis* Kovar-Eder sp. nov. (leaves) and *Trapa ungeri* Wójcicki & Kovar-Eder sp. nov. (fruits) are described for the first time.

KEY WORDS: leaves, *Trapa* fruits, fossil flora, Pannonian, Miocene, Hausruck, Upper Austria

INTRODUCTION

The Hausruck lignite area has been exploited for more than two centuries. Small coal-bearing pits were very numerous, although this mining area never attained significant economic importance. Earlier authors such as Hofmann (1929) described *Taxodioxylon sequoianum* Hofmann, *Taxodioxylon taxodioides* (Merklin) Gothan, *Cupressinoxylon hausruckianum* Hofmann, and *Osmundites schemnicensis* Pettko (see also Hofmann 1926). From the western part of the Hausruck lignite area, pollen were investigated by Klaus (1952). Klaus (1977) listed pollen taxa from the Heissler Stollen in the Illing area north of Hinterschlagen when he described a cone of *Pinus spinosa* Herbst. Knobloch (1977, 1981) listed leaf taxa and described fruits and seeds from dumps of the mine Schmitzberg near Ampflwang. Weber and Weiss (1983) and Groiss (1989) summarized the mining history of and the scientific approaches to the Hausruck lignite area. Kovar-Eder (1988) described leaf assemblages from three gravel pits in the Kobernausser Wald, the adjacent region towards the west-southwest. The here presented flora from the opencast mine Heissler constitutes a new fragment in the puzzle-like vegetation pattern that accompanied the Hausruck/Kobernaussen fluviatile system. Its more than regional significance is self-evident due to the hitherto unknown floristic composition.

GEOGRAPHIC AND GEOLOGICAL BACKGROUND

The Hausruck lignite area extends from Haag in the northeast to Ampflwang in the southwest, Thomasroith in the south and to Wolfsegg in the southeast (Figs 1, 2). To the west it extends over Altsommerau almost to the road connecting Frankenburg and Ried. The Hausruck lignite-bearing sequence – Hausruck-Kohleton Series, Kohleführende Süsswasserschichten (Aberer 1958) – is developed above marine pelites (“Schlier”) of Early Miocene age (Central Paratethys stage Ottnangian). The Hausruck gravels cover the

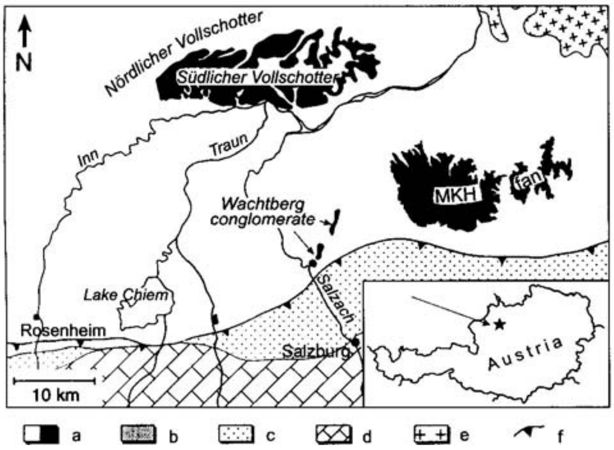

Fig. 1. Geographic location of the Hausruck lignite area [eastern part of the Munderfing-Kobernaussen-Hausruck (MKH) fan]; from Brügel (1998: Fig. 9), modified. **a** – Autochthonous Molasse, **b** – Folded Molasse, **c** – Rhenodanubian Flysch + Helvetic zone, **d** – Northern Calcareous Alps, **e** – Bohemian Massif, **f** – Alpine front

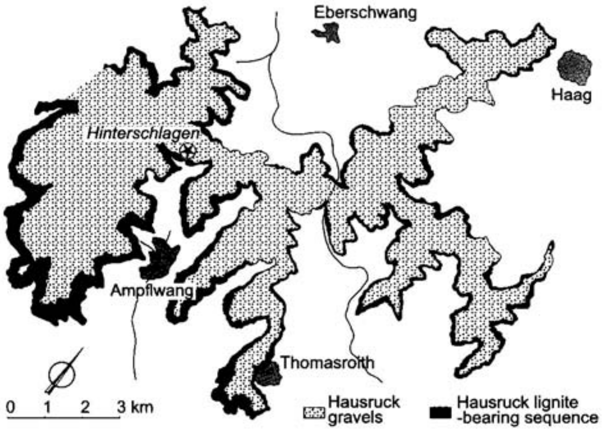

Fig. 2. Overview of the Hausruck lignite area and location of the opencast mine Heissler –⊛; from Pohl (1968: Pl. 1) and Weber and Weiss (1983: Fig. 73), modified

lignite-bearing sequence. The sequence reaches up to 60 m thickness and bears three coal seams up to 7 m thick.

Towards the west-southwest the Hausruck lignite-bearing sequence intercalates with the Kobernaussen gravels. The latter represent the central, high-energy facies within the Hausruck/Kobernaussen fluviatile system, whereas the former represents the marginal, low-energy, fine-grained facies.

The Kobernaussen gravels indicate sediment transport from the Eastern Alps towards the NW, changing with the overlying Hausruck gravels to the NE, which is related to the formation of the present-day axial slope of the Eastern Alpine foreland and eastern directed drainage system (Mackenbach 1984). According to Brügel (1998) the Munderfing-Kobernaussen-Hausruck fan is a remnant of the Palaeo-Inn drainage system which had its source in the Bergell region (Ober Engadin). (The term Munderfing-Kobernaussen-Hausruck fan also includes the Munderfing gravels.) *Hipparion primigenium* (H.v. Meyer) from the Hausruck lignite-bearing sequence in Wolfsegg (Thenius 1952) is indicative of Pannonian age (Late Miocene; higher parts of the Hausruck lignite-bearing sequence). *Anchitherium aurelianense* (Cuv.) and *Tetralophodon longirostris* (Kaup) from the Kobernaussen gravels support this age (Thenius 1952, Jenisch & Tichy 1977). *Stegotetrabelodon grandincisivum* Schl., *Tetralophodon longirostris/arvensis* (Cr. & Job.), and *Dicerorhinus schleiermacheri* Kaup from the Hausruck gravels indicate a slightly younger age (Rabeder in Papp et al. 1985). In Haag/Hausruck a vertebrate fauna has recently been discovered in the Hausruck gravels. This fauna may provide new information on the stratigraphic position of these deposits (G. Daxner-Höck pers. comm.).

The small openpit Heissler near Hinterschlagen of the Wolfsegg-Traunthaler Kohlenwerke A.G. was situated about 2 km NW of Ampflwang in the Hausruck (Upper Austria) at 13°33′04″ E longitude and 48°06′45″ N latitude according to Austromap (Austrian Map). The deposits there were part of the Hausruck lignite-bearing sequence. Fieldwork was done in 1988. From bottom to top the sedimentary sequence was composed of:

0–3.00 m kaolinitic, muscovite-rich, silty fine-sand with gravel components, gray-yellowish gray
3.00–3.20 m muscovite-rich fine-sand, gray to brownish with gray lenses; plant detritus
3.20–6.50 m massive brown coal with thin lenses of lignitic clays
6.50–6.85 m clay lacking macroscopically visible muscovite particles; wood fragments
6.85–9.05 m massive brown coal
9.05–9.75 m clay, black-brownish, brown; rich in plant detritus
9.75–9.80 m browncoal

9.80–10.80 m clay, gray, in the upper 0.3 m rich in plant remains, leaf-bearing horizons

10.80–11.60 m clay, gray, light gray, blue-gray, rich in plant remains, leaf-bearing horizons

11.60–12.10 m clay, brown, partly with plant-bearing horizons

12.10–14.30 m massive brown coal with a fusite layer in its upper part

14.30–15.30 m sands, gravels, not in situ.

MATERIAL AND METHODS

The samples were carefully dissolved in water to isolate the leaves. The remaining sediment was then sieved for diaspores. The leaves were put on slides, embedded in glycerol and covered with a thin plastic foil.

As the leaves were entirely black with no venation details visible, some were made transparent by using a 2–3% hydrogen peroxide solution to which some glycerol was added. This mixture with leaves included was slowly heated to 60–70°C for between several minutes to half an hour (depending on how quickly bleaching took place). When the leaves were brownish/transparent they were carefully washed with water and again embedded on slides in glycerol and covered by a plastic foil.

Cuticles were prepared primarily from fragments lacking gross-morphological criteria for determination. This should guarantee to identify also rare taxa and such with rather low preservational potential.

In some cases cuticles were obtained by putting fragments of leaves treated in this manner in a drop of glycerol with 5% KOH-solution. Usually, however, cuticle preparations were done using Schulze's reagents ($KClO_3$+HNO_3) followed by treatment in 5% KOH-solution. The cuticles were partly stained with safranin and embedded in glycerol.

Table 1. List of samples and corresponding collection file numbers

Sample Nos	Coll. file Nos leaves	Coll. file Nos *Trapa*
E-Hischla 88/1		
E-Hischla 88/2	1999B0002	2001B0010
E-Hischla 88/3		
E-Hischla 88/4	1999B0060	
E-Hischla 88/5	1999B0001	
E-Hischla 88/6		2000B0014
E-Hischla 88/7		2001B0011
E-Hischla 88/8	1999B0043	
E-Hischla 88/9		
E-Hischla 88/10		1988/0138

The material studied now comprises the macro remains (leaves and *Trapa* fruits). The results obtained from the diaspore record will be published later. The material is housed in the palaeobotanical collection of the Naturhistorisches Museum Wien (sample Nos and coll. file Nos see Tab. 1).

SYSTEMATIC PART

Cupressaceae

Tetraclinis salicornioides (Unger) Z. Kvaček

Pl. 1 fig. 5

1841 *Thuites salicornioides* Ung.; Unger, p. 11–13, Pl. 2 figs 1–4.
1989 *Tetraclinis salicornioides* (Unger) comb. nov. Z. Kvaček, p. 45–52, Pl. 1 fig. 11, Pl. 2 figs 2–14, Pl. 3 figs 3, 4.

Material. Coll. file No. 1999B0001/756.

Remarks. This single twig segment is remarkable because *T. salicornioides* was already very rare during the Late Miocene of Central Europe compared to the Middle and Early Miocene record.

Taxodiaceae

Taxodium dubium (Sternberg) Heer

Pl. 1 figs 1–4, Pl. 3 figs 1, 2

1823 *Phyllites dubius* Sternb.; Sternberg, p. 37, Pl. 36 fig. 3.
1853 *Taxodium dubium* (Sternb.) Heer; Heer, p. 136.

Material. Cuticles investigated, coll. file Nos 1999B0001/604, 673, 725, 726, 731, 734; 1999B0043/31, 90.

Determinations based on gross morphology only, coll. file Nos 1999B0001/68, 529–534, 536–583, 585–590, 592–601, 603, 605–613, 615–633, 636–663, 666–672, 674–687, 690–706, 708–724, 727, 728, 732, 733, 735–737, 749; 1999B0002/18–24 (18 twig fragments); 1999B0043/1, 2, 4–30, 32–89, 91–121, 125–154; 1999B0060/1–27.

Description. Mainly terminal leafy shoots of lanceolate shape, gradually tapering towards the base and the apex; needles alternately arranged, distichous, often some of them missing, needles up to 9 mm long, 0.9–1.2 mm wide; needle apex mostly acute, sometimes slightly rounded, needle base mostly somewhat narrowed, twisted and then decurrent on the shoot axis, needles amphistomatic;

cuticle delicate, stomata arranged in two bands laterally of the central vein both on the ad- and abaxial leaf side, only the needle margins and the central vein are stomata-free zones; there the non-modified epidermal cells are well cutinized and rather elongated, while the non-modified epidermal cells of the stomata zones are less strongly cutinized and not or only slightly elongated; cuticular flanges of non-modified epidermal cells somewhat irregularly cutinized, straight to slightly undulate; stomata usually oriented transversally/obliquely to the needle length, stomata cyclocytic, stomata length in submacerated state 37–45 µm, aperture length 16–18 µm; aperture length in fully macerated state 24–28(34) µm; T-shaped polar thickenings well developed, preserved in submacerated state only.

Remarks. Among the numerous twigs, most match the characteristic taxodioid foliage and only few twigs have cupressoid needles. The cuticles of the taxodioid twigs match the description of Kvaček (1976) and Worobiec and Lesiak (1998). Therefore, we suggest that all remains belong to *T. dubium* although the presence of *Glyptostrobus* among the cupressoid twigs cannot be ruled out completely. In the fruit and seed record, cones and seeds of *Taxodium dubium* are also very abundant while remnants of *Glyptostrobus* are extremely rare.

Betulaceae

Alnus menzelii Raniecka-Bobrowska

Fig. 3: 7–9, Pl. 1 figs 14–18, Pl. 4 figs 2–8

?1852 *Alnus diluviana* Ung.; Unger, p. 106, Pl. 16 figs 16, 17.
1954 *Alnus menzelii* Raniecka-Bobrowska sp. nov.; Raniecka-Bobrowska, p. 11, fig. 4, phot. 11–13.

Material. Determination based on gross morphology and cuticles, coll. file Nos 1999B0002/3, 26; 1999B0043/168, 177, 200, 225, 232, 259, 261, 266, 267, 269, 276, 281, 282, 286, 288, 290–292, 296, 298, 303.

Determination based on gross morphology only, coll. file Nos 1999B0001/130, 346, 478, 486; 1999B0043/253, 254, 263, 271, 274, 278, 279, 283, 287, 293–295, 297, 299–301, 304–307, 309, 310, 401, 406, 411.

?*Alnus menzelii,* coll. file Nos 1999B0043/163, 175, 178, 196.

Description. Fragments of simple leaves, lamina elliptic, base cordate, usually somewhat asymmetric, petiole rarely preserved, incomplete 4–5 mm long, in No. 1999B0043/291 15 mm long, apex not preserved; leaf margin double serrate, several smaller teeth (up to 7) developed between adjacent primary ones; one of the secondary teeth is commonly developed exactly in the sinus of two first order ones, sinus and apex usually acute; venation simple craspedodromous; midvein straight, slender; secondaries slender, arising usually in distances of 7–10 mm (around the maximum width of the lamina) and angles of (40)45–60°, running almost straight, slightly diverging towards the leaf margin, entering the first order teeth centrally; opadial veins (see Liu 1996) present; tertiaries arising almost at right angles from the secondaries, oblique, largely parallel to each other, percurrent, forked percurrent; marginal tertiaries may supply second order teeth, but commonly they form marginal loops from which finer veins run into second order teeth; fourth order venation still distinctive, forming an irregular meshwork in which the next order veins form a fine reticulum; areoles without free-ending veinlets, as well as with sometimes unforked sometimes forked, free-ending ones; ultimate marginal veins looped. Several leaves show characteristic feeding traces – oval holes between the secondary veins (Pl. 1 fig. 16); cuticles of both leaf surfaces thin; occasional faint striation developed above veins; adaxial cuticule thin, non-modified epidermal cells straight-walled, with slender, regularly cutinized anticlines; in No. 1999B0043/303 the surface is striate; abaxial cuticle thin, non-modified epidermal cells largely straight-walled, anticlines somewhat stronger cutinized than adaxially; size of non-modified epidermal cells 7–24 µm, average 13–20 µm; stomatal complexes anomocytic, stomatal length (15)18–24(28) µm, average 20–23 µm, stomatal width 11–20(23) µm, average 15–18 µm, ratio length/width (0.9)1–2; stomatal aperture spindle-shaped with well-cutinized, smooth outer stomatal ledges, length of stomatal aperture (8)11–16(21) µm, average 12–17 µm; pluri-cellular trichome bases present, mostly consisting of four cells, rarely less and occasionally consisting of more cells (five to seven); diameter of trichome bases 18–31 µm; simple trichome bases with trichome remains

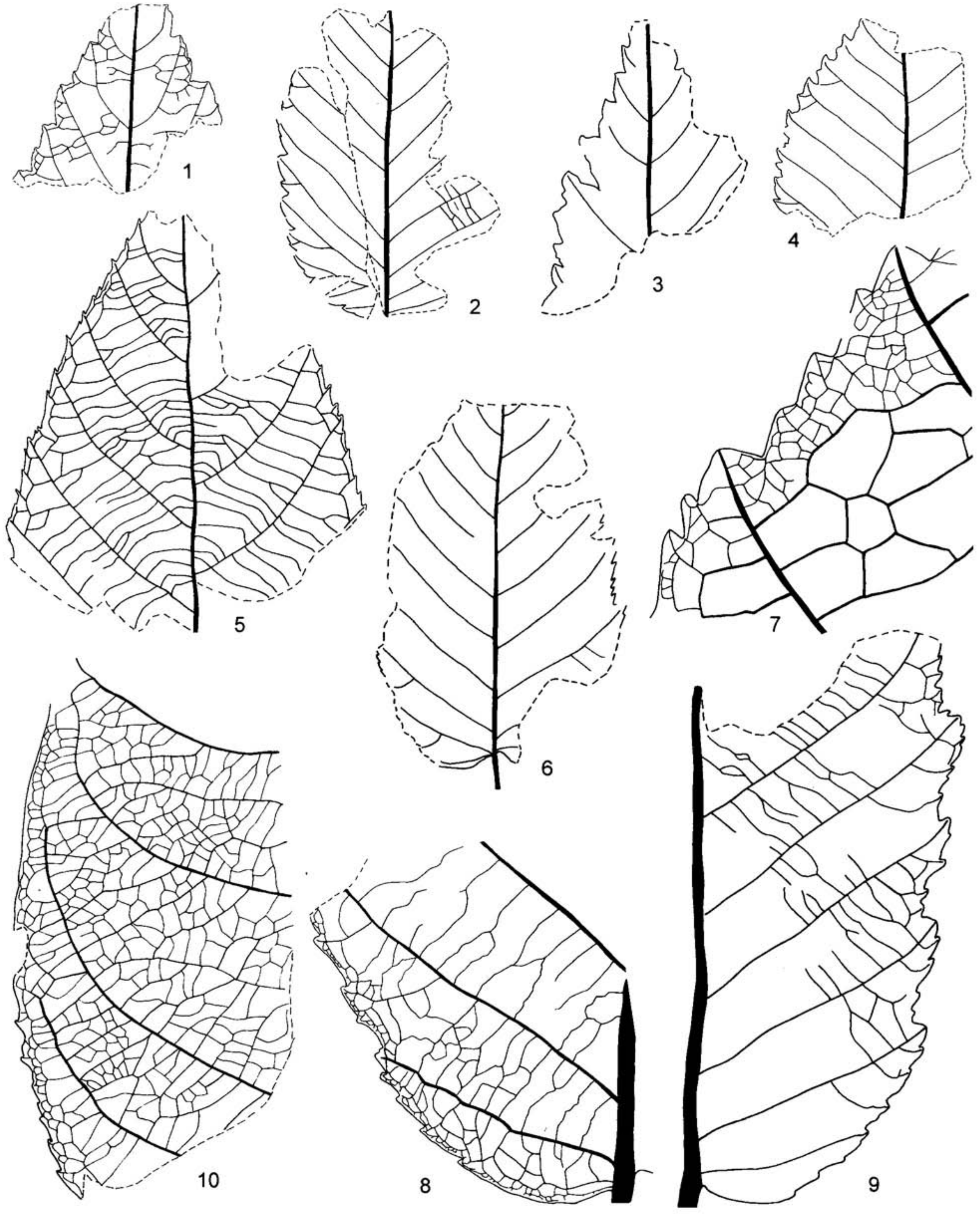

Fig. 3. *Zelkova zelkovifolia* (Unger) Bůžek & Kotlaba: **1** – No. 1999B0043/284, × 2. *Dicotylophyllum* sp.: **2** – No. 1999B0043/257, × 1. *Ulmus* sp.: **3** – No. 1999B0043/275, × 2; **4** – No. 1999B0001/10, × 2. *Alnus julianiformis* (Sternberg) Z. Kvaček & Holý: **5** – No. 1999B0043/245, × 1.5. *Alnus diluviana* Unger: **6** – St. Stefan near Graz, syntype of Unger (1852: Pl.16 fig.16) Landesmuseum Joanneum No. 77 607, × 1. *Alnus menzelii* Raniecka-Bobrowska: **7** – No. 1999B0043/292, × 10; **8** – No. 1999B0043/267, × 3; **9** – No. 1999B0043/296, × 2. *Salix hausruckensis* Kovar-Eder sp. nov.: **10** – paratype, No. 1999B0043/397, × 3

sometimes still attached also present, diameter of the almost circular trichome pores (6)10–17(20) µm; see Tab. 2.

Remarks. The complex of features is decisive for the distinction of these leaves from *Betula*: four-celled trichome bases are more

Table 2. Measurements of cuticular features of the described Betulaceae. STL – stomata length, STB – stomata width, STL/STB – relation of stomata length to width, STA – aperture length, USZK – size of non-modified epidermal cells abaxially, OSZK – size of non-modified epidermal cells adaxially, TB – diameter of trichome pore/base; av. – average values of these parameters have been counted only if a minimum of five values were available. If possible, ten measurements of each parameter in each leaf were counted, $^{x)}$ < ten measurements, $^{y)}$ < five measurements, $^{z)}$ only one measurement

Coll. file Nos	STL in µm	av.STL in µm	STB in µm	av.STB in µm	STL/STB	STA in µm	av.STA in µm	USZK in µm	av.USZK in µm	simple TB in µm	av.simple TB in µm	pluri-cell.TB in µm	av.pluri-cell.TB in µm	OSZK in µm	av.OSZK in µm
							Alnus menzelii								
1999B0043/168	17–22	20	13–18	16	1.1–1.4	9–12	11	8–16	12			22–32$^{x)}$	24$^{x)}$		
1999B0043/267	18–34	23	13–23	17	1.0–1.9	12–21	17	15–24	20	7–17$^{x)}$	13$^{x)}$	24$^{y)}$			
1999B0043/269	18–23$^{x)}$	21$^{x)}$	17–20$^{x)}$	18$^{x)}$	1.0–1.2$^{x)}$	11–15$^{x)}$	13$^{x)}$	13–23	18	6$^{z)}$		21–27$^{y)}$		16–24	22
1999B0043/281	19–28$^{x)}$	23$^{x)}$	12–17$^{x)}$	15$^{x)}$	1.1–2.0$^{x)}$	11–16$^{x)}$	13$^{x)}$	7–17$^{x)}$	13$^{x)}$	10–17$^{y)}$		23$^{z)}$		13–23	18
1999B0043/290	15–24	20	11–20	16	0.9–1.4(2)	8–15	12	12–24	18	12–20$^{y)}$		21–31$^{y)}$			
1999B0043/292	21–24$^{y)}$		13–16$^{y)}$		1.3–1.8$^{y)}$	13–18$^{y)}$		12–24	18			18–24$^{x)}$	22$^{x)}$	21–29(37)	24
1999B0043/296	19–23$^{y)}$		15–18$^{y)}$		1.3–1.5$^{y)}$	13–16$^{y)}$		10–24$^{x)}$	17$^{x)}$	12–13$^{y)}$				15–24	20
							Alnus julianiformis								
1999B0043/245	15–22$^{y)}$		15–18$^{y)}$		0.8–1.2 $^{y)}$	7–11$^{x)}$	9$^{x)}$					15–24 (28)	19		
							Alnus vel *Betula* sp.								
1999B0043/218	16–24	21	(11)13–20	16	1.0–1.9	(8)11–18	14	18–43	27	intercostally 12–22; upon veins 6–12$^{x)}$	17 9$^{x)}$	21–24$^{y)}$			

common than more-celled ones, opadial veins are present, while pectinal ones are absent; the secondary veins penetrate centrally in the first order teeth (Liu 1996). Gross-morphologically these leaves match very well with *Alnus menzelii*. However, due to the better preservation the material described here shows more venation details than other leaves so far described (Knobloch 1986, Hummel 1991, Belz & Mosbrugger 1994, Worobiec & Lesiak 1998, Zastawniak & Walther 1998). Marginally, the tertiary veins occasionally run into the second-order teeth, but they often form marginal loops from which finer veins arise and end in tiny teeth. Although the first order teeth are usually thicker than the second order ones, they are occasionally of almost the same size.

The best preserved cuticle is from a fragment (No. 1999B0043/168) lacking any gross-morphological characteristics (Pl. 4 fig. 5). The features match well with those from *A. menzelii*, only the length of the stomatal aperture seems a little smaller (Tab. 2). The leaf margin of specimen No. 1999B0043/303 is less characteristic of *A. menzelii*, but the cuticle matches well. Only in this specimen striation has been found on the adaxial cuticle (Pl. 4 fig. 7) as has been described by Belz and Mosbrugger (1994). The specimens from Bełchatów also bear a striate adaxial cuticle (G. Worobiec pers. comm.).

Knobloch (1986) already mentioned similarities between *A. menzelii* and *A. diluviana* Unger 1852. One of the syntypes of *Alnus diluviana* Unger (1852: p. 106, Pl. 16 fig. 16) from St. Stefan (Styria, Sarmatian, Middle Miocene), still existing in the collection of the Landesmuseum Joanneum (palaeontological collection, coll. file No. 77.607), was reinvestigated. This specimen is an imprint with only very tiny remains of the carbonized lamina (Fig. 3: 6). The leaf margin is preserved in only two areas (one on the left, the other on the right side of the lamina). The margin to right clearly shows several small teeth between two adjacent first order teeth and the leaf base is distinctly cordate. Although only the midvein, the second order venation, and probably few finer veins are preserved, this leaf in fact very closely resembles *A. menzelii*. Cuticle preparations yielded only fragments lacking diagnostic features: the area above the midvein with longitudinally arranged cells. The type material of *A. menzelii* from Konin (Raniecka-Bobrowska 1954) is covered with lacquer and no cuticles have yet been investigated (G. Worobiec pers. comm.). In summary, the probability that *A. diluviana* is the older synonym of *A. menzelii* is quite high, although due to the poor preservation of the type specimen we hesitate to fuse the two species.

Alnus julianiformis (Sternberg) Z. Kvaček & Holý

Fig. 3: 5, Pl. 1 fig. 8, Pl. 4 fig. 1

1823 *Phyllites julianaeformis* Sternb.; Sternberg, p. 37, 39, Pl. 36 fig. 2.

1974 *Alnus julianaeformis* (Sternb.) Z. Kvaček & Holý; Kvaček and Holý, text-fig. 1, Pls 1–3, Pl. 4 fig. 1.

Material. Determination based on gross morphology and cuticle, coll. file No. 1999B0043/245.

Description. Apical part of the lamina 47 mm long, 40 mm wide; leaf margin double serrate, teeth tiny, acute, first order teeth not essentially bigger than second order ones; venation simple craspedodromous, midvein slender, slightly wavy, due to the origins of the secondaries; secondaries slender, somewhat curved, arising in distances of 8–11 mm and under angles of 45–60°; tertiaries (forked-) percurrent, oblique; marginally finer veins arise from the tertiaries and enter the second order teeth; fourth order veins forming a polygonal network in which the fifth order veins enclose the areoles, free-ending veinlets in the areoles rarely visible (possibly not well preserved); cuticules of both leaf surfaces very thin, poorly preserved even in submacerated state: mostly four-celled trichome bases, rather common upon veins, their diameter 15–24(28) µm; non-modified epidermal cells on the (?) lower leaf surface almost straight walled, on the (?) upper leaf surface slightly wavy; stomata faintly visible, rather small, 15–22 µm long, 15–18 µm wide, aperture slightly stronger cutinized, 7–11 µm long.

Remarks. Among the rich material only this leaf can be assigned to *Alnus julianiformis*. Its distinct gross morphology (especially the leaf margin) and the cuticular features clearly justify the separation from the bulk of the Betulaceae leaves. Compared with the leaves of *Alnus menzelii* the four-celled trichome bases appear more commonly situated upon the veins in *A. julianiformis*.

Alnus vel ***Betula*** sp.

Pl. 3 figs 7, 8

Material. Cuticle investigated, coll file No. 1999B0043/218.

Description. One fragment, the middle part of a lamina with serrate margin; adaxial cuticle not preserved; abaxial cuticle delicate, yet preserved in bigger fragments; non-modified cells with thin but equally developed, straight to slightly curved anticlines, size of non-modified cells 18–35(43) µm, average 27 µm; stomatal complexes anomocytic, stomata weakly cutinized, often only faintly visible, only the outer cuticular ledges of the aperture are slightly stronger cutinized and often have a well-staining membrane that sometimes disintegrates from the cuticle; stoma length 13–24 µm, average 21 µm, stoma width (11)13–20 µm, average 16 µm, relation length/width 1.0–1.9, aperture length (8)11–18 µm; three types of trichome bases are to be distinguished: rarely occurring four- and five-celled bases, their diameter 21–24 µm; simple ones mainly on main veins with pores of 6–12 µm in diameter, average 9 µm; trichome bases mainly on thin veins/intercostal areas with pores of 12–20(22) µm diameter, average 17 µm, the pores are girdled by a ring of cells smaller than the non-modified ones, these cells are slightly thicker and often but not necessarily somewhat radially elongated; one trichome is preserved: very delicate, unicellular, 58 µm long.

Remarks. This gross-morphologically indeterminable fragment bears cuticular features that allow a distinction from all the other Betulaceae remains described here: The epidermal walls of the guard cells are only faintly developed, in contrast to *A. menzelii*. A distinctly staining membrane upon the stomatal aperture as observed in this specimen has not been encountered for *A. menzelii*. Simple trichome bases with big pores have been found in the specimen No. 1999B0043/290 assigned to *A. menzelii*. However, in the specimen described here (No. 1999B0043/218) there are two distinct sizes of simple trichome bases in addition to the pluricellular ones. Although the cuticular features are quite well preserved, a closer determination is not possible.

Betulaceae gen. et sp. indet.

Material. Cuticles investigated, coll. file Nos 1999B0002/2, 4, 27–31, 33–36.

Coll. file Nos 1999B0043/186, 188, 189, 195, 201, 206, 214, 215, 233, 241, 243, 244, 246, 256, 260, 264, 273, 277.

Here we fuse numerous specimens which lack distinctive features. They may as well belong to *Alnus menzelii*.

Fagaceae

Quercus kubinyii (Kovats ex Ettingshausen) Czeczott

Pl. 1 figs 10, 11, Pl. 3 figs 5, 6

1852 *Castanea kubinyi* Kov.; Ettingshausen, p. 6, Pl. 6 fig. 12.

1951 *Quercus kubinyi* (Kov.); Czeczott; Czeczott, p. 392, fig. 7.

Material. Determination based on gross morphology and cuticle in coll. file No. 1999B0001/516; determination based on gross morphology only in coll. file No. 1999B0001/419.

Description. No. 1999B0001/516 leaf fragment with three very distinct attenuate marginal teeth, sinus rounded; venation simple craspedodromous, tertiaries forked percurrent; petiole largely complete, 12 mm long; adaxial cuticle delicate, anticlines somewhat irregularly developed, somewhat wavy, cell size 24–45 µm, average 36 µm, a small-celled hypodermis is well developed, hypodermal cell size 7–15 µm, average 11 µm; abaxial cuticle delicate, stomatal complexes anomocytic, very densely spaced; stomata oval, length 21–28 µm, average 24 µm, width 16–24 µm, average 20 µm, ratio length/width 1.1–1.5, stomatal aperture slender oval, length 8–15 µm, average 11 µm, polar T-thickenings more or less well developed, poles emarginate; simple, round to oval-shaped trichome bases, sometimes in pairs, diameter 8–15 µm, average 11 µm, their margin moderately thickened, very thin remains of uniserate mono- to pluricellular trichomes still attached; No. 1999B0001/419: petiole 6 mm long, lamina elliptic, 31 mm long (apex missing), 16 mm wide, base probably rounded, margin simple/? double serrate, single teeth relatively widely spaced, of different shape, bases acute, apices partly acute (rounded), partly incomplete; venation ? craspedodromous, secondaries widely spaced 6–11 mm; tertiaries forked percurrent; cuticle not preserved.

Remarks. Both leaves are gross-morphologically not very well preserved. However, the cuticle of leaf No. 1999B0001/516 and the leaf margin in combination with the cuticular features justify the assignment. The cuticle matches well with those described by Knobloch and Kvaček (1976) for *Quercus kubinyii* from the Wackersdorf area (Germany), although the stomata and the non-modified epidermal cells of the adaxial cuticle are bigger in our material.

Ulmaceae

Ulmus sp.

Fig. 3: 3, 4, Pl. 1 figs 9, 9a

Material. Coll. file Nos 1999B0001/10; 1999B0043/222, 275, 280.

Description. Fragments with double-serrate leaf margin, first order teeth bigger than second order ones, the basal sides of the teeth are convex or acuminate and the apical sides acuminate or concave, venation simple craspedodromous.

Remarks. According to the shape of the leaf margin these three fragments can be assigned to *Ulmus*. They may belong to *Ulmus carpinoides* Goeppert emend. Menzel (Goeppert 1855, Menzel 1906). No cuticle is preserved.

Zelkova zelkovifolia (Unger) Bůžek & Kotlaba in Kotlaba

Fig. 3: 1, Pl. 1 figs 12, 12a

1843 *Ulmus zelkovaefolia* Ung.; Unger, p. 94–95; Pl. 24 fig. 7 pro parte, figs 9–12, Pl. 26 fig. 7.

1963 *Zelkova zelkovaefolia* (Unger) Bůžek & Kotlaba; Kotlaba, p. 59–62, Pl. 3 figs 7, 8.

Material. Coll. file No. 1999B0043/284.

Description. An apical fragment of a lamina with few, relatively big-sized marginal teeth, basal and apical sides of the teeth acuminate; single secondary order teeth also developed; venation simple craspedodromous, running in wide curves across the lamina, originating in distances of 6 mm and under angles of 45–55°.

Remarks. This fragment is distinguished from the fragments of *Ulmus* by bigger and fewer teeth as well as their different shape. The cuticle is not preserved.

Salicaceae

Salix hausruckensis Kovar-Eder **sp. nov.**

Fig. 3: 10, Pl. 2, 5, Pl. 6 fig. 12

Holotype. Coll. file No. 1999B0001/9, Pl. 2 fig. 6, Pl. 5 fig. 8.

Paratypes. Coll. file Nos 1999B0001/13, 21, 23, 261, 285; 1999B0043, 326, 328, 397, 408, 410; Fig. 3: 10, Pl. 2 figs 1–5, 7–10, Pl. 5 figs 4–7, Pl. 6 fig. 12.

Type locality. Tagebau Heissler near Hinterschlagen, Hausruck lignite area, Upper Austria.

Level. Clayey seam parting below the upper seam in the opencast mine Heissler, Hausruck lignite-bearing sequence.

Age. Miocene, Pannonian.

Derivatio nominis. From the geographic region and lignite mining area Hausruck in Upper Austria, where this species has been discovered.

Further material. Cuticles investigated, coll. file Nos 1999B0001/2, 4–8, 11–20, 22, 24–28, 59, 62; 1999B0002/1, 5, 7–15, 17, 25; 1999B0043/156–161, 164, 166, 167, 170, 171, 176, 179, 181–185, 187, 190, 192–194, 197, 199, 202–205, 208, 209, 211, 213, 216, 219, 220, 223, 224, 226, 227, 229–231, 237, 238, 240, 333, 412.

Determinations based on gross morphology only, coll. file Nos 1999B0001/29, 31–36, 38, 39, 41–49, 51–57, 60, 63, 65–67, 72, 81–92, 94–98, 101, 103–105, 107, 111, 112, 115–118, 122–129, 131, 133–138, 140, 141, 144–147, 149–151, 153, 156–159, 161–163, 165–167, 169, 170, 172–174, 176–186, 188, 189, 192–203, 205, 206, 208–216, 219–231, 234–238, 240–242, 244, 245, 247–258, 262–269, 271–277, 281–284, 286–301, 303, 305, 307, 310, 311, 313–315, 319–322, 324, 325, 327, 328, 330–332, 334–337, 339–343, 345, 347–355, 357, 363, 364, 366, 368–370, 372–374, 376, 377, 380–382, 384, 385, 387–391, 394, 395, 397, 400, 402, 404, 408, 411, 412, 414–416, 420–426, 428–432, 434–437, 439–444, 446–449, 452, 455, 457–461, 464–468, 470–477, 479, 482–485, 487–491, 493–513, 517, 519, 522, 524, 525, 528; 1999B0043/314–325, 327, 329–332, 334, 336, 338–345, 347–372, 375–391, 393–396, 398–400, 402–405, 407, 409, 413–417.

Description. Lamina wide elliptic, up to at least 150 mm long and 66 mm wide, relation length/width 1.7–2.5; petiole up to 47 mm long, often curved and basally broadened, adaxially clustered glands on the distal part of the petiole; leaf base sometimes somewhat cordate and slightly asymmetric, obtuse, rounded; apex acute, acuminate, sometimes attenuate; leaf margin regularly, simply serrate from the base up to the middle or two-thirds of the lamina with glands adherent to the margin, apically often but not always entire; in small leaves only the base is serrate, then the margin is entire; teeth tiny, regularly spaced with rounded or acute bases and rounded apices; venation brochidodromous, distance between secondaries in the middle of the leaves 7–16 mm, in small leaves 3–4 mm, angles of origin at the base of big leaves between 70–90°, towards the apex about 40–50°, in smaller leaves generally 40–50°, secondaries forming wide curves, at the margin they form loops; loops of higher venation orders send fine veins towards the bases of the teeth from where these run along the apical sides of the teeth towards the teeth apices; tertiary veins forked percurrent, oblique; fourth order venation distinctive, polygonally reticulate, occasionally (forked-)percurrent between the tertiaries; fifth order veins forming polygonals, areoles with several branched veinlets; adaxial cuticle thick, cell-outlines sometimes formed of thick and straight-running anticlines, in other leaves the anticlines are hardly traceable on the thick cuticle; cell outlines commonly 4–6-sided, more rarely polygonal; trichome bases absent; size of non-modified epidermal cells (7)12–24 µm, average 16–18 µm; faint epicuticular striation upon veins and occasionally in intercostal areas; abaxial cuticle thick, non-modified epidermal cells with thick anticlines, occasionally not equally developed, running straight, size of non-modified epidermal cells (7)11–28 µm, average 12–16(21) µm; stomatal complexes brachyparacytic to cyclocytic (especially the giant stomatal complexes); stomata oval, stomatal length 10(12)-30 µm, average 19–21 µm, width (7)12–22 µm, average 13–16 µm; stomatal aperture spindle-shaped, almost

Table 3. Comparison of the fossil *Salix hausruckensis* Kovar-Eder sp. nov. with gross-morphologically similar, contemporary species

Character: / Species	petiole length	shape of blade	length	width	relation l/w	margin	base	apex	indumentum
Salix hausruckensis sp. nov.	≤ 47, indumentum variable, apical glands clustered	elliptic	≥ 150	≥ 66	1,7–2,5	regularly simple serrate, glands adherent, apically and small leaves often entire	(slightly asymmetric) cordate, obtuse, rounded	acute, acuminate, (attenuate)	adaxially glabrous, abaxially density of trichome bases variable
Sect. *Brewerianae* Schneider									
Salix hookeriana	10, hairy	elliptic	40–110	20–50	~2–2,2	without teeth or coarsely, wavy toothed	mostly rounded	rounded, bluntly mucronate	adaxially nearly glabrous, abaxially hairy
Sect. *Floridanae* Dorn / Humboldtianae Pax in Engler & Prantl / Tetraspermae (Andersson) C.K. Schneider in Sargent									
Salix floridana	16–43, indumentum variable, apical glands and two lateral glanduliferous leaflets	elliptic, (oblong, ovate)	90–190	40–80	2,1–2,4–3(4)	glandular serrate, teeth with irregular shape, glands patulous, occasionally parts entire	rounded, slightly cordate and asymmetric	acute, rarely acuminate	adaxially hairy, abaxially hairy along primary vein, then glabrous
Sect. *Magnificae* C.K. Schneider in Sargent									
Salix magnifica	≦ 40, glabrous, no glands	elliptic, ovate, obovate-oblong	≦ 200	≦ 110	~ 1,8	entire when young; irregularly glandular serrulate	rounded, subcordate, (broadly cuneate or attenuate)	rounded, obtuse, mucronate, acute	glabrous
Salix moupinensis	< 17, young hairy then glabrecent, one apical gland	oblong, elliptic, obovate, ovate	130	60	~ 1,8	glandular serrate, glands patulous	rounded to cuneate	acute, shortly acuminate	glabrous, hairy along veins when young
Sect. *Psilostigmatae* C.K. Schneider in Sargent									
Salix fargesii	≤ 15, usually several glands	elliptic, narrowly ovate	110	60	~1,8	glandular serrulate	rounded to cuneate	acute to rounded	adaxially glabrous or hairy, abaxially hairy along veins
Sect. *Tetraspermae* (Andersson) C.K. Schneider in Sargent									
Salix tetrasperma	10–15, glabrous	ovate, linear lanceolate	60–160	25–45	~2,4–3,5	serrate	cuneate, suborbicular	acuminate	glabrous

reaching the poles, outer cuticular ledges strongly thickened, aperture length (6)8–22 (25) µm, average 13–19 µm; epidermal walls of the guard cells sometimes well developed, sometimes hardly recognizable; giant stomata present, length >30 µm, aperture length 28–30 µm, sometimes radial striation present laterally; commonly the stomata show double contours; abundance of trichome bases variable: in some leaves almost restricted to the veins, in others also scattered in the intercostal areas; simple trichome pores, 4–15 µm in diameter, average 6–10 µm, surrounded by small, thickly cutinized cells, trichome bases raised volcano-like above the surface; faint striation upon main veins.

Discussion. The rich leaf material shows rather homogeneous morphological features concerning leaf size and shape including the base and the apex, the long and glanduliferous petiole as well as the regularly and distinctly toothed leaf margin with transition to entire margin at the apex. These features allow the clear distinction from other fossil *Salix* species.

Among the about 500 living species, large and elliptic/wide elliptic leaves (ratio length/width 1.5–2.9) are not very common. Among these are *Salix fargesii* Burkh., *S. hookeriana* Barratt, *S. magnifica* Hemsl., and *S. moupinensis* Franch. But there are also distinct differences between these species and *S. hausruckensis* in features such as the petiolar length, the presence of distal petiolar glands, and the leaf margin (Tab. 3).

The southeast American *Salix floridana* Chapman (description see Argus 1986) was found to most closely resemble the fossils described here (Pl. 6 figs 10, 11). This concerns all the gross-morphological features described for S. *hausruckensis* except the irregular marginal serration with patulous glands and the leaflet-like glanduliferous wings developed in addition to the distal petiolar glands (adaxial leaf surface) of *S. floridana* leaves. Moreover, the cuticular structures of *S. floridana* resemble closely those of *S. hausruckensis* except for the size of the non-modified epidermal cells on both leaf surfaces, which is larger in *S. floridana* (Tab. 4, Pl. 6 figs 13, 14). *S. floridana* is close to the sect. *Humboldtianae* Pax in Engler & Prantl. However, Dorn (1976) placed *S. floridana* in the monotypic section *Floridanae* Dorn. Argus (1986) prefered to place it

Table 4. Measurements of cuticular features of *Salix hausruckensis* Kovar-Eder sp. nov. and *Salix floridana* Chapman. STL – stomata length, STB – stomata width, STL/STB – relation of stomata length to width, STA – aperture length, USZK – size of non-modified epidermal cells abaxially, OSZK – size of non-modified epidermal cells adaxially, TB – diameter of trichome pore/base; av. – average values of these parameters have been counted only if a minimum of five values were available. Ten measurements of each parameter in each leaf were counted, $^{z)}$ only one measurement

Coll. file Nos	STL in µm	av. STL in µm	STB in µm	av.STB in µm	STL/STB	STA in µm	av.STA in µm	giant STL in µm	giant STB in µm	giant STA in µm	USZK in µm	av.USZK in µm	TB in µm	av.TB in µm	OSZK in µm	av.OSZK in µm
Salix hausruckensis																
1998B0001/9	15–27	21	12–22	16	0.9–1.5	15–25	19				11–21	15	7–12	9	8–18	16
1999B0001/13	12–30	21	12–18	13	1.0–1.9	8–22	16	33$^{z)}$		29$^{z)}$	12–27	21	2–10	7	12–24	16
1999B0043/397	10–29	19	7–18	13	(0.7) 1.1–1.8 (2.4)	6–20	14				7–23	12	6–15	9	12–24	18
1999B0043/408	15–26	20	12–16	13	1.1–1.7	11–18	13	31$^{z)}$	18$^{z)}$	28$^{z)}$	11–28	16	6–12	10	7–22	17
1999B0043/410	12–24	19	12–18	14	1.0–1.9	8–17	14			30$^{z)}$	7–26	14	4–9	6	12–24	17
Salix floridana																
	16–24	19	(9)11–16	12	1.4–1.9 (2.1)	12–16	13				21–37	27	10–17	14	17–34	28

within sect. *Humboldtianae*, but proposed that, if it is to be separated, it should be placed into sect. *Tetraspermae* (Anderson) C. Schneider in Sargent. In the latter, *S. tetrasperma* is a large-leafed species, but petiolar glands are not described and the petiole is distinctly shorter (Wu & Raven 1999) than in *S. hausruckensis*. Later, Argus (1997) followed Dorn (1976) placing S. *floridana* in the section *Floridanae.* Sample coll. file No. 1999B0001 which was especially rich in *S. hausruckensis* leaves contained also dehisced capsules of *Salix*.

Herbarium material studied

Salix floridana Chapman; Ocala National Forest, Florida, Coll. W. Buechler, Boise, Idaho.

Salix hookeriana Barrat; Oregon, Lane County; Darlingtonia Botanical Wayside State Park, 8.9 km from Florence, at jct. of US 101 and Mercer Lake Road. *Gaultheria–Vaccinium* community; infrequent. Marie Jeannette James 96, Lee Michalson; 27 July 1991 (WU).

Salix japonica Thunb.; Flora japonica, ex Hb. Bot. Inst. Sci. Coll. Imp. Univ. Kyoto; Japonia: Prov. Sagami, Hakone; 28.7.1934, leg. Z. Toshiro (WU).

Salix magnifica Hemsl.; Tien-chu-hsien, Szechuan; leg. K.L. Chu No. 2811; 14 Juni 1936 (W).

Trapaceae

The best preserved *Trapa* fruits were collected by splitting loose blocks (not in situ). Washed samples mainly yielded fragments that were typically not determinable at the species level.

Trapa ungeri Wójcicki & Kovar-Eder **sp. nov.**

Fig. 4: 1–6, Pl. 6 figs 1–5

Holotype. Coll. file No. 2000B0014/1 (Fig. 4: 1, Pl. 6 fig. 2)

Paratypes. Coll. file Nos 2000B0014/2–4 1988/0138/3 A, B, 6 (Fig. 4: 2–6, Pl. 6 figs 1, 3–5)

Type locality. Tagebau Heissler near Hinterschlagen, Hausruck lignite area, Upper Austria.

Level. Clayey seam parting below the upper seam in the opencast mine Heissler, Hausruck lignite-bearing sequence.

Age. Miocene, Pannonian.

Derivatio nominis. Named in honour of the Austrian botanist F.J.A.N. Unger (1800–1870), in recognition of his substantial contribution to European palaeobotany.

Description. Fruits slender, broadly obtriangular in outline with four horns; fruit 5.5–11.0 mm high (including neck), width 20–38 mm (including upper horns); fruit about 1/4 to 1/3 as high as wide; head of the fruit pronounced, located below the margin of the upper horns; fruit head gradually attenuating into a conical, truncate neck of up to 3 mm length, usually slightly protruding from the upper horns; corona lacking; apical aperture 1.5–2.5 mm in diameter; a ring of upward pointing hairs closing the apical aperture usually visible; surface of the fruit head and neck finely ribbed; upper horns widely expanded, usually sword-shaped, 6–15 mm long, raised at the base, with characteristic conical tubercles at the base on the apical side of the horns, tubercles up to 1.5 mm long, upper horns gradually continuing into thin, reflexedly barbed spines (harpoons), 5–11 mm long; presence of mat areas excluded (in Latin *areolae impressae* – morphological structures present in some *Trapa* species at the base and/or apical part of the upper horns); lower horns narrowly ligulate in outline, strongly reflexed, straight, about 3–12 mm long, located approximately in the centre of the fruit body or somewhat below, usually with small, conical tubercles near the base, tubercles up to 0.8 mm long; at the base of the lower horn a small cavity is usually developed; frame of the fruit (in Latin *linea* [*costa*] *media*; in German *Hauptrippe* – protruding rib between upper and lower horns framing the fruit head) well pronounced with solid tubercles located between the upper and lower horns, tubercles 1.5–4.0 mm long and up to 1.5 mm wide near the base, their upper part sometimes dichotomously forked; basal part of the fruit body obtriangular truncate in outline with a few protruding longitudinal ribs; basal ring not developed; margin of the fruit base usually irregular; basal scar up to 1.5 mm in diameter.

Discussion. *Trapa ungeri* represents a new fruit morphotype that has not been reported previously among extant *Trapa* or in the fossil record (e.g. Nakano 1914, Flerov 1926, Vassilev 1949, 1973, Miki 1952, Janković 1958,

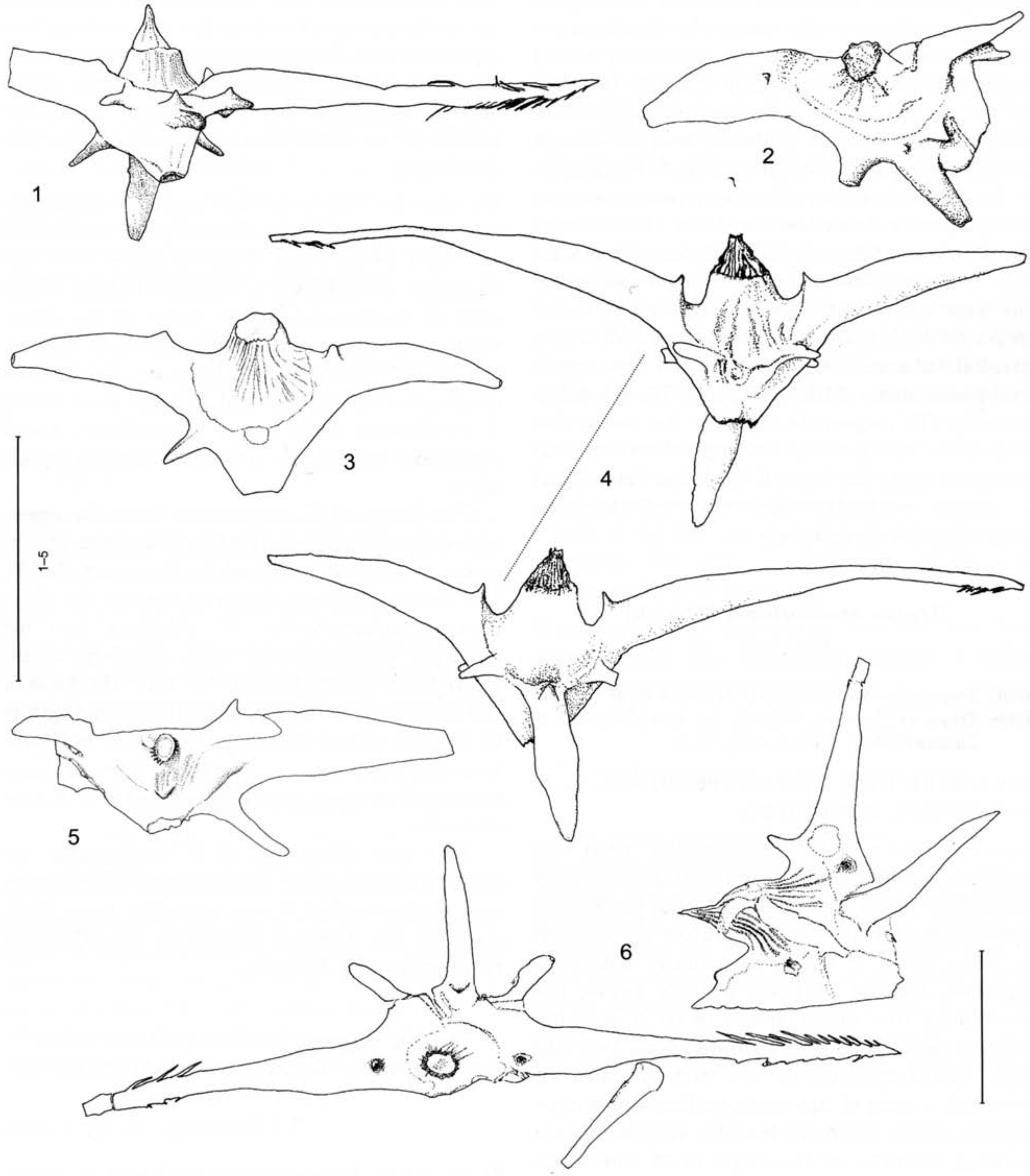

Fig. 4. *Trapa ungeri* Wójcicki & Kovar-Eder sp. nov.; scale bar 1 cm. **1** – holotype, No. 2000B0014/1; **2–6** – paratypes, **2** – No. 2000B0014/3, **3** – No. 1988/0138/6, **4** – No. 2000B0014/2, **5** – No. 2000B0014/4, **6** – No. 1988/0138/3A, B

Kovar 1979, Mai 1985, Givulescu & Ticleanu 1986, Kadono 1987, Kovar-Eder 1988, Kovar-Eder & Krainer 1988, 1990, Verdcourt 1998, Wójcicki et al. 1999). It shows no close relationship with any known member of the genus and it can be distinguished from other species of the genus by: very long sword-shaped upper horns, the relatively short fruit, the relation of fruit height/width 1/4 to 1/3, the relatively broad conical, truncate neck, the presence of additional tubercles near the base of the upper and lower horns, long, sometimes dichotomously forked tubercles between the upper and lower horns, the narrowly ligulate, reflexed lower horns and the relatively broad basal scar with an irregular margin. Because of the very unique character combination, *Trapa ungeri* should probably be placed in a new, monotypic, above-species unit (section?).

In single characters *T. ungeri* resembles two fossil species described by Miki (1952) from the Pliocene of Japan: *T. octotuberculata* Miki has characteristic tubercles developed near the base on the distal side of the upper horns (Miki 1952, Fig. 6A); *T. pulvinipoda* Miki has divided tubercles located between the upper and lower horns (Miki 1952, Fig. 7A, B). Additionally, *T. ungeri* is similar to both the Japanese species by having short conical tubercles near the base of the lower horns, but it differs evidently from both of them in general gross morphology.

Trapa srodoniana Wójcicki

Pl. 6 fig. 6

1990 *Trapa silesiaca* Goeppert; Stuchlik et al., Pl. 14.
1998 *Trapa srodoniana* Wójcicki sp. nov.; Wójcicki & Zastawniak, p. 170, textfig. 3a-i.

Material. Coll. file Nos 1988/0138/1, 7, 8, 2001B0010/2, 2000B0014/5.

Description. Fruit obtriangular with two massive, extended horns; fruit 10–14 mm high (including neck), width 16–24 mm (including upper horns); fruits approximately 2/3 as high as wide; head of the fruit usually well pronounced, located at least slightly below the margin of the upper horns with a well-developed neck, both finely ribbed; neck 1–2 mm high; apical aperture up to 3 mm in diameter, rounded, a ring of upward pointing hairs closing the apical aperture usually visible; corona lacking; surface of the fruit head and neck finely ribbed; upper horns slightly upward pointing to patent, shape narrowly triangular, raised at the base with a smooth apical side of the horn's margin, upper horns 6–8 mm long, sometimes distally bearing damaged thin spines; presence of mat areas not excluded; lower horns reduced to tubercle-like structures, probably rounded, up to 2 mm long, located usually at the middle or above the centre of the body of the fruit; tubercles present between the upper and lower horns, up to 1 mm long and up to 1.2 mm wide near base; lower part of the fruit body obtriangular in outline, its surface covered with a few protruding, longitudinal ribs; fruit base characteristically abruptly narrowed, terminating in a very small scar or elongated into a "petiolate" basal appendix of up to 1.5 mm length; basal ring not developed.

Remarks. There are at least five specimens that fit very well into the range of variability of *Trapa srodoniana* Wójcicki 1998 from the Pliocene of Bełchatów, Middle Poland (Wójcicki & Zastawniak 1998). Some of the specimens from the opencast mine Heissler support the interpretation given there in the species diagnosis that the elongated basal part of the *T. srodoniana* fruit bears a "petiolate", basal appendix lacking in the other known specimens.

The fruits of *T. srodoniana* from the opencast mine Heissler evidently differ from *T. silesiaca* as originally defined by Goeppert (1855). The basic difference concerns some of the diagnostic characteristics. *T. silesiaca* has for example well-developed solid, regularly triangular lower horns located 1/4 from the base of the fruit body or below, is regularly triangular in outline with a relatively small but well-pronounced basal scar, and lacks an abruptly narrowing fruit base as is characteristic of *T. srodoniana*.

The new discovery of *T. srodoniana* redefines its age as far back as to the Pannonian and suggests that it was probably more common in the Central European Mio-Pliocene than previously thought.

Trapa ungeri Wójcicki & Kovar-Eder **sp. nov. / *T. srodoniana*** Wójcicki – putative hybrids

Pl. 6 figs 7–9

Material. Rich material that will be specified separately, e.g. coll. file Nos 1988/0138/2, 4, 5.

In addition to the above-described species, the material from the opencast mine Heissler is rich in intermediate forms. Their variability suggests the presence of *Trapa ungeri* and *T. srodoniana* hybrids and seems to be even characteristic of a hybrid swarm as is well known from modern *Trapa* (e.g. Staszkiewicz & Wójcicki 1979, Kadono 1987, Tzvelev 1993). The intermediate character of *T. ungeri*/*T. srodo-*

niana-fruits is especially well expressed in the general fruit shape, that of the fruit base and the lower horns, the presence of characteristic, conical tubercles near the base on the distal margin of the upper horns as well as in the presence of solid, apically sometimes dichotomously forked tubercles between the upper and lower horns. The *Trapa* material from the opencast mine Heissler is the subject of ongoing intensive systematic studies that will be presented in a separate publication.

Aceraceae

Acer tricuspidatum Bronn

Pl. 1 figs 6, 7, Pl. 3 fig. 4

1838 *Acer tricuspidatum* Bronn; Bronn, Pl. 35 fig. 10a, b.

Material. Cuticles investigated, coll. file Nos 1999B0001/406, 453; 1999B0043/165, 198, 221, 228, 234, 236, 239, 248–252.

Description. See Walther (1972).

Remarks. The characteristic cuticular structures unambiguously allow the determination even of gross-morphologically indeterminable fragments.

Dicotylophyllum sp.

Fig. 3: 2, Pl. 1 fig. 13, Pl. 3 fig. 3

Material. Coll. file Nos 1999B0043/257, 268.

Description. Specimen No. 257: lamina elliptic or slightly ovate, 50 mm long (completed about 60 mm long), 40 mm wide; base and apex unpreserved; leaf margin double serrate, whereby the first order teeth are distinctly bigger than the second order ones; basal and apical sides of first and second order teeth convex to ? acuminate, sinus acute, tooth apex ? complete, either rounded or acute/acuminate; venation simple craspedodromous; secondaries originating in the middle of the lamina at distances of 6–8 mm, running almost straight into the first order teeth; from the secondaries smaller veins fork towards the base and run into the second order teeth; tertiaries oblique, forked percurrent; fourth order and higher order venation forming a rectangular/pentagonal network; adaxial cuticle not preserved; abaxial cuticle very delicate, non-modified epidermal cells with slender but equally developed anticlines, forming straight-walled polygonal cell outlines; stomata ?anomocytic, the epidermal walls of the guard cells are hardly traceable, while the relatively short oval apertures are clearly visible; aperture length 7–12 µm; no trichome bases observed; specimen No. 268 is a fragment of the leaf margin with few teeth only.

Remarks. The cuticles of Nos 257 and 268 are identical. The systematic affinity of these leaf fragments remains unclear.

TAPHONOMY AND ECOLOGY

The plant-bearing layers were developed in the middle and upper part of a clayey seam parting. The overall common feature is the dominance of *Taxodium dubium*. Although species-poor, the floristic composition (Tab. 5) does not indicate major facial differences. The partly excellent preservation of the fossil remains in the clayey sediment (see Pl. 2) and the co-occurrence of leaves/twigs and fructifi-

Table 5. The leaf spectrum

Sample Nos E-Hischla	2	4	5	8
Coll. file Nos	1999B0002	1999B0060	1999B0001	1999B0043
Tetraclinis salicornioides			1	
Taxodium dubium	18	27	>100	>100
Alnus menzelii	2		4	48+ ?4
Alnus julianiformis				1
Alnus vel *Betula* sp.				1
Betulaceae gen. et sp. indet.	11			18
Quercus kubinyii			2	
Ulmus sp.			1	3
Zelkova zelkovifolia				1
Salix hausruckensis	12		>100	>100
Acer tricuspidatum			2	12
Dicotylophyllum sp.				2

cations of *Taxodium* and *Salix* indicate almost (par)autochthonous conditions. This fact along with the presence and partly the abundance of leaves/twigs of *Taxodium dubium*, *Salix hausruckensis*, *Alnus menzelii*, and *Acer tricuspidatum* and the well-preserved *Trapa* remains point towards quiet conditions in a swamp and floodplain environment with shallow open waters.

In this context, note that broad-leafed *Salix* species in Europe today are more characteristic of low-energy fluviatile environments and stagnant wetland habitats, whereas slender-leafed species are typically bound to channel-near environments. The latter habitats are subject to frequent flooding with relatively high flow energy, and slender-leafed species are better equipped to retain their leaves undamaged (E. Hübl pers. comm.). This adaption to variable facies may already have been differentiated in the Late Miocene because in Schneegattern in the Kobernausser Wald a mass-occurrence of the slender-leafed *Salix lavateri* A. Braun emend. Hantke was described associated with abundant *Alnus ducalis* Gaudin emend. Knobloch, indicating softwood riparian forests. There, the sediments are part of the Kobernaussen gravels, representing the central, higher-energy deposits that intercalate with the marginal, low-energy Hausruck lignite-bearing sequence (see also “Geographic and geological background”).

A morphologically very close counterpart of *Salix hausruckensis* is *Salix floridana*, a subtropical, Tertiary relict endemic to a few disjunct areas of Central and North Florida and adjacent parts of Georgia. The small trees of this species are bound to wet and often flooded soils in swamps and along streams and rivers (Argus 1986). This matches also the requirements of *Taxodium distichum* (L.) Rich., the close relative of the fossil *T. dubium*, which is dominant along with *Salix hausruckensis* in the leaf record of the opencast mine Heissler near Hinterschlagen. However, we lack information about the associates of this rare, modern willow in natural habitats.

The taxa documented here do not offer insight into the flora on natural levees and zonal habitats. Only *Tetraclinis salicornioides* (one single twig fragment) may represent a zonal element. However, the pollen record from the “Heissler Stollen” (Hausruck lignite-bearing sequence) reported by Klaus (1977) as well as the plant assemblages from the Kobernaussen gravels (Kovar-Eder 1988) provided evidence of riparian forests and habitats on natural levees comparable to hinterland forests in the region of the Hausruck/Kobernaussen fluviatile system.

COMPARISON WITH THE PLANT RECORD FROM SCHMITZBERG NW HINTERSCHLAGEN/HAUSRUCK
(Knobloch 1977, 1981)

The fossil assemblage from the Schmitzberg area is species-poorer in the leaf record. Although most taxa represent azonal conditions, this flora differs in its most abundant element *Glyptostrobus europaeus* from that of the opencast mine Heissler. In the leaf record, agreement is restricted to the documentation of *Alnus*. These discrepancies indicate diverse azonal habitats.

COMPARISON WITH THE FLORA OF KONIN (Raniecka-Bobrowska 1954)

The flora of Konin [lowermost part of the Poznań clays = Gray Clay Member at the base of the Poznań Formation (Ważynska 1998)] shows striking floristic slimilarity with that from the opencast mine Heissler near Hinterschlagen. Both floras derive from clays and share the prevalence of azonal taxa. They have in common the low number of leaf species, among which they share the abundance of *Alnus menzelii* and the presence of *Trapa*. While *Taxodium dubium* is the dominant conifer in the opencast mine Heissler, the dominant form in Konin is *Glyptostrobus europaeus*, both represented by twigs, cones and seeds. Based on the figured specimens (Raniecka-Bobrowska 1954: Fig. 7, phot. 21–23) we suspect that the abundant leaves of *Polygonum miosinicum* Hu & Chaney from Konin may in fact represent *Salix*. If so, this would be another feature matching the flora from the opencast mine Heissler. However, in Konin the plant-bearing clays are developed above the coal seam, indicating the basin’s successive subsidence there, while in the opencast mine Heissler the plant-bearing layers are restricted to the upper part of a clayey seam parting, indicating increasingly more shallow conditions.

CONCLUSIONS

1. A flora is reported from the upper part of a clayey seam parting from the opencast mine Heissler near Hinterschlagen in the Hausruck lignite area in Upper Austria. According to earlier mammal findings in the Hausruck/Kobernaussen complex the stratigraphic position of these deposits is regarded as Upper Miocene, Pannonian.

2. Based on the mass occurrence of leaves, *Salix hausruckensis* Kovar-Eder is described for the first time. No close fossil species is known to us. As the closest living relative, *Salix floridana* Chapman, a relict species with disjunct distribution in Florida and Georgia, was detected.

3. *Trapa ungeri* Wójcicki & Kovar-Eder is a new fossil waternut species described here that resembles in some respects the fossil Japanese species *T. octotuberculata* Miki and *T. pulvinipoda* Miki. The rich *Trapa* material also comprises *T. srodoniana* Wójcicki and many specimens that may represent a hybrid swarm of these two species.

4. The taphonomical setting indicates short or almost no transport for most of the leaf material (almost autochthonous conditions). Along with the floristic spectrum, this indicates waterlogged and quiet conditions in a swamp and floodplain environment with shallow open waters in which *Taxodium dubium*, and *Salix hausruckensis,* were most abundant associated with *Alnus menzelii.*

ACKNOWLEDGEMENTS

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PLATES

Plate 1

Taxodium dubium (Sternberg) Heer

1. No. 1999B0001/673
2. No. 1999B0043/90
3. No. 1999B0043/98
4. No. 1999B0043/58

Tetraclinis salicornioides (Unger) Z. Kvaček

5. No. 1999B0001/756, × 4

Acer tricuspidatum Bronn

6. No. 1999B0001/453
7. No. 1999B0043/165

Alnus julianiformis (Sternberg) Z. Kvaček & Holy

8. No. 1999B0043/245
   8a. Details of the leaf margin and venation × 2

Ulmus sp.

9. No. 1999B0001/10
   9a. × 2

Quercus kubinyii (Kovats ex Ettingshausen) Czeczott

10. No. 1999B0001/516
11. No. 1999B0001/419

Zelkova zelkovifolia (Unger) Bůžek & Kotlaba

12. No. 1999B0043/284
    12a. × 1.5

Dicotylophyllum sp.

13. No. 1999B0043/257

Alnus menzelii Raniecka-Bobrowska

14. No. 1999B0043/296
    14a. Details of venation and leaf margin, × 2
15. No. 1999B0043/292
    15a. × 2
16. No. 1999B0043/266
    16a. Details of venation and leaf margin, × 2
17. No. 1999B0043/281
    17a. Details of venation and leaf margin, × 2
18. No. 1999B0043/267
    18a. Details of venation and leaf margin, × 5

Unless otherwise stated × 1


1
2
3
4
5
6
7
8
8a
9
9a
10
11
12
12a
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14a
15
15a
16
16a
17
17a
18
18a

Plate 2

Salix hausruckensis Kovar-Eder sp. nov.

1. Paratype, small leaf, largely entire-margined except at the base, No. 1999B0001/13
2. Paratype, acuminate leaf apex, entire margined, in the lower part, left hand, regularly simply serrate, No. 1999B0043/397
   2a. Details of the venation, × 5
3. Paratype, apical half of a lamina, in its lower part regularly serrate, at the acuminate apex entire margined, No. 1999B0043/326
4. Paratype, an acute/acuminate leaf apex, entire-margined, No. 1999B0001/285
5. Paratype, apical half of a lamina, simply regularly serrate, except the entire margined acuminate/attenuate apex, No. 1999B0001/21
6. Holotype, basal half of an elliptic, regularly serrate leaf margin, long petiole, No. 1999B0001/9
7. Paratype, lower two-thirds of an elliptic lamina with petiole; base slightly asymmetric, regularly, simple serrate margin, No. 1999B0001/23
8. Paratype rounded leaf base with long petiole of a large leaf. No. 1999B0043/328 and No. 1999B0043/408

9, 10. Paratypes, elliptic laminae of rather large leaves No. 1999B0043/410
9a, 10a. Details of the venation and the leaf margin, secondary veins forming loops near the leaf margin, tertiary veins forked percurrent, at the margin also forming smaller loops, from which finer veins originate and enter the teeth bases, still finer veins run towards the teeth apices
9a. × 5
10a. × 2

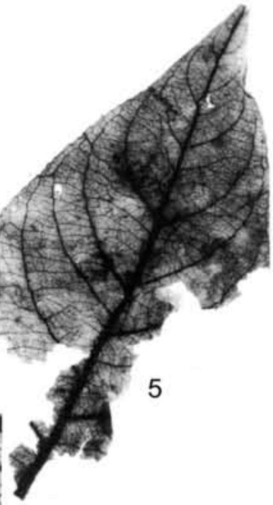
Unless otherwise stated × 1


1


2


3


4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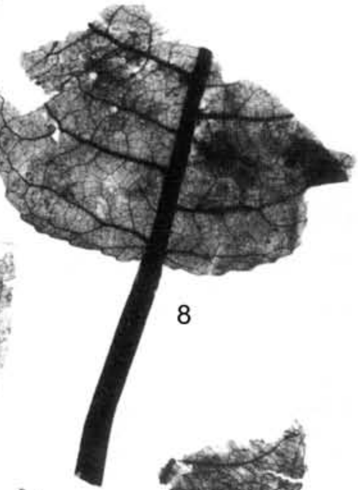
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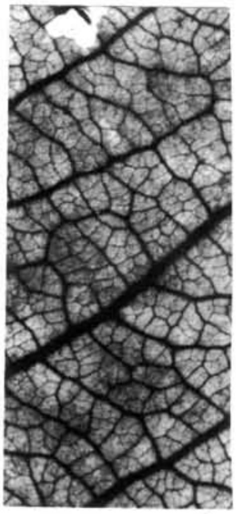
6


7


9a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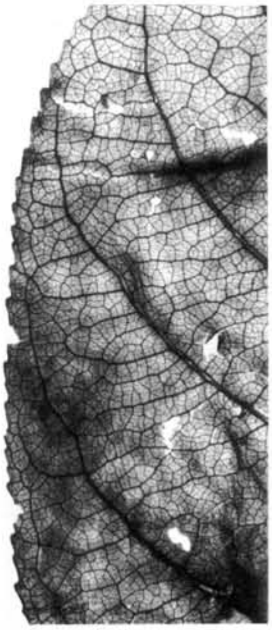
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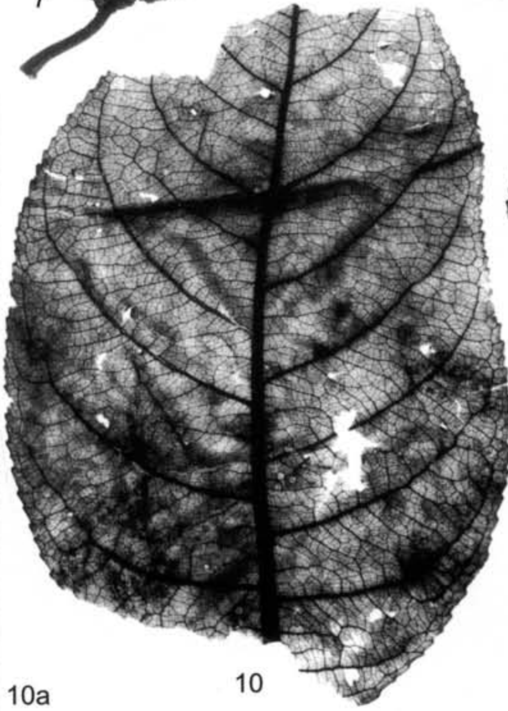
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9

Plate 3

Taxodium dubium (Sternberg) Heer

1. A submacerated needle, the stomata with polar T-thickenings preserved, stomata oblique/transversally oriented, situated ab- and adaxially in two zones right and left hand of the main vein, marginal areas of the needle without stomata, No. 1999B0043/31/2, × 200
2. A fully macerated cuticle, stomata oriented oblique/transversally, No. 1999B0043/90/1, × 200

Dicotylophyllum sp.

3. Abaxial cuticle, No. 1999B0043/257/1

Acer tricuspidatum Bronn

4. Abaxial cuticle with several trichomes, No. 1999B0043/250/1

Quercus kubinyii (Kovats ex Ettingshausen) Czeczott

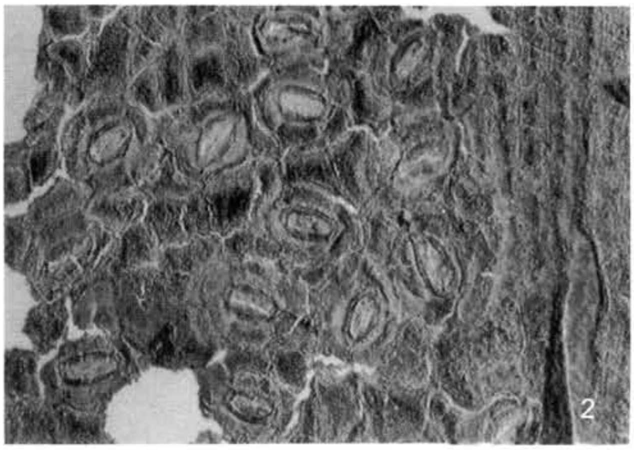
5, 6. No. 1999B0001/516/4
   5. Abaxial cuticle with anomocytic stomatal complexes
   6. Adaxial cuticle with distinct small-celled hypodermis

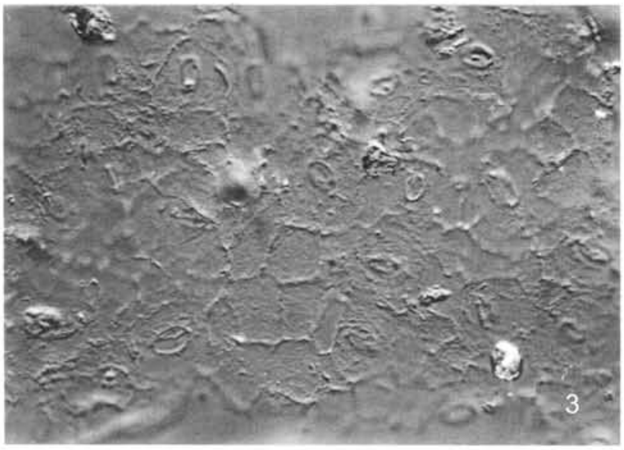
Alnus vel *Betula* sp.

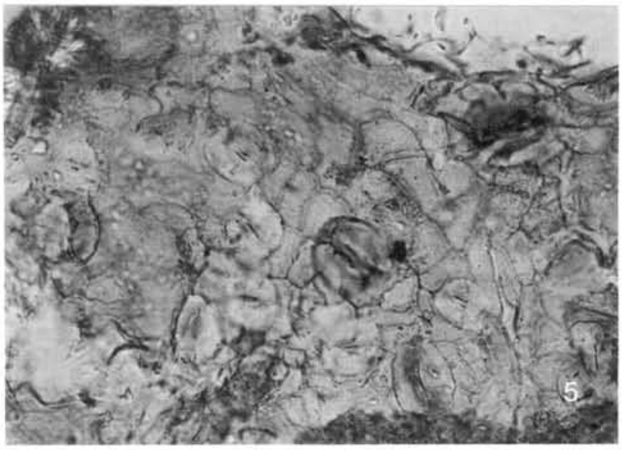
7, 8. No. 1999B0043/218/2
   7. Abaxial cuticle with big simple trichome bases and basal trichome remains, anomocytic stomatal complexes with distinctly staining ledges that are already missing on some stomata
   8. Abaxial cuticle without trichome bases, stomata partly with well-staining ledges still attached, partly they have already disintegrated, × 200

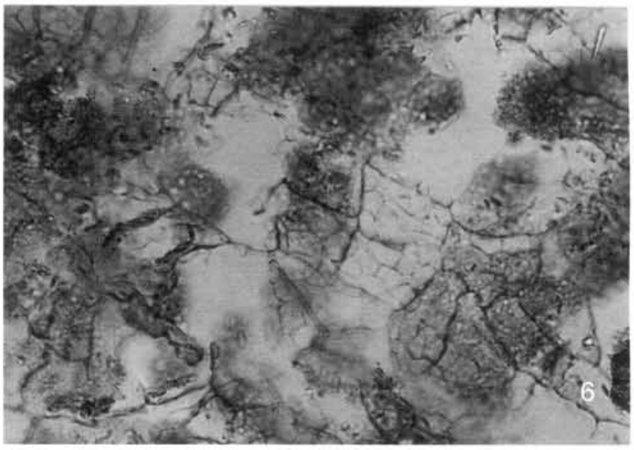
Unless otherwise stated × 400

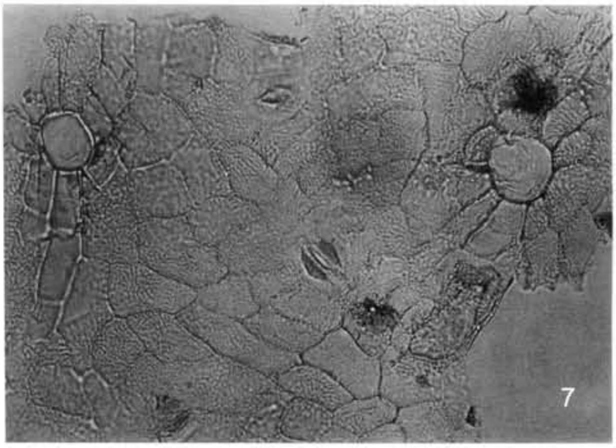
Plate 3











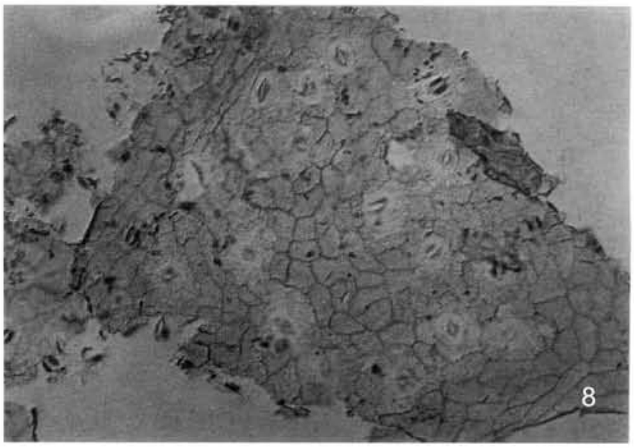


Plate 4

Alnus julianiformis (Sternberg) Z. Kvaček & Holy

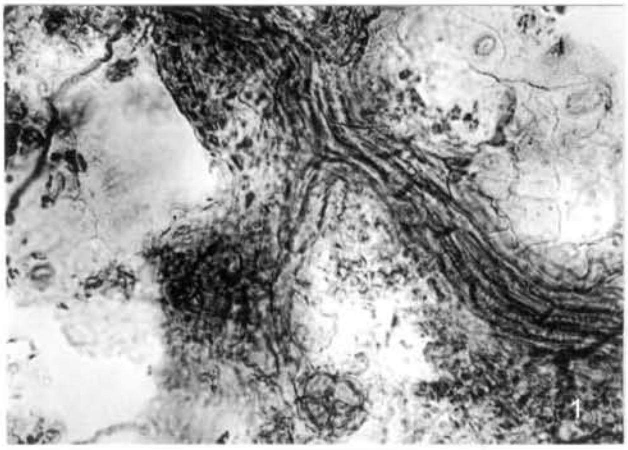
1. Abaxial cuticle, only in submacerated state stomata are visible, four-celled trichome base, No. 1999B0043/245

Alnus menzelii Raniecka-Bobrowska

2–6. Abaxial cuticle, non-modified epidermal cells straight-walled
  2. Anomocytic stoma and simple trichome bases, lower right with two simple trichomes still attached, No. 1999B0043/267/2
  3. Anomocytic stomatal complexes and simple trichome base, No. 1999B0043/296/1
  4. Four-celled trichome base and anomocytic stomatal complex, No. 1999B0043/276/1
  5. Exceptionally well-preserved cuticle of a fragment lacking gross-morphologically significant features, anomocytic stomatal complexes, four-celled trichome base, No. 1999B0043/168/1
  6. Anomocytic stomatal complexes, sizes rather variable, No. 1999B0043/281/1

7, 8. Adaxial cuticle, non-modified epidermal cells straight-walled
  7. With cuticular striation, No. 1999B0043/303/1
  8. No. 1999B0043/292/1

All figures × 400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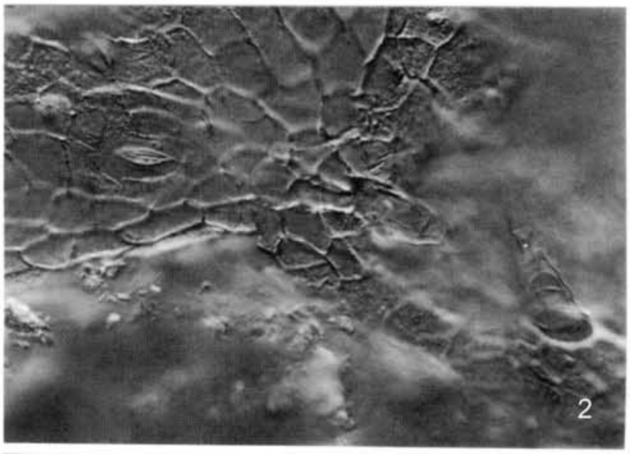
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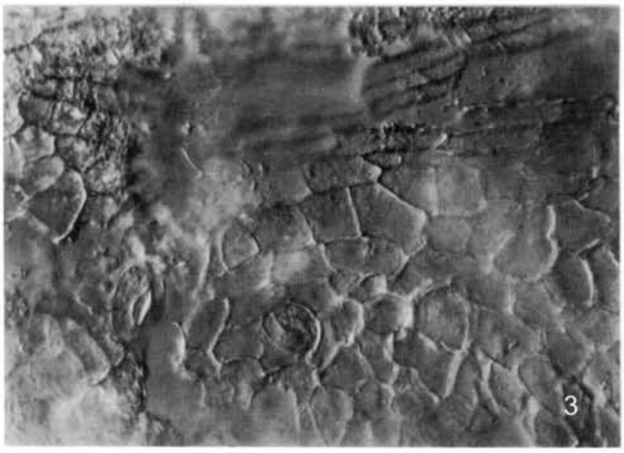
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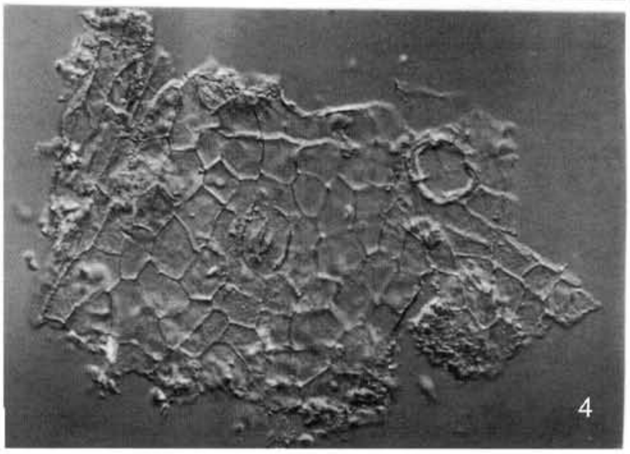
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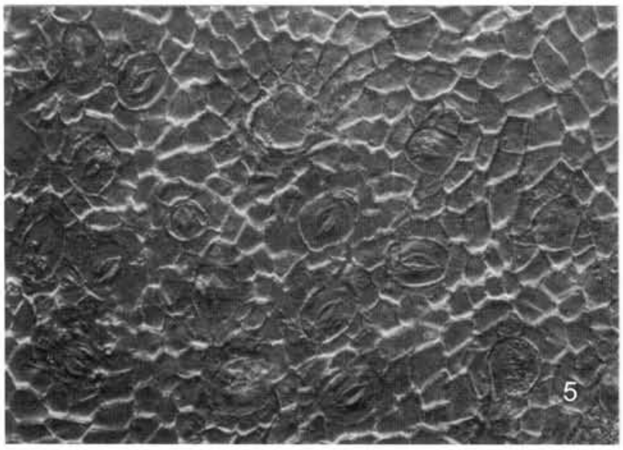
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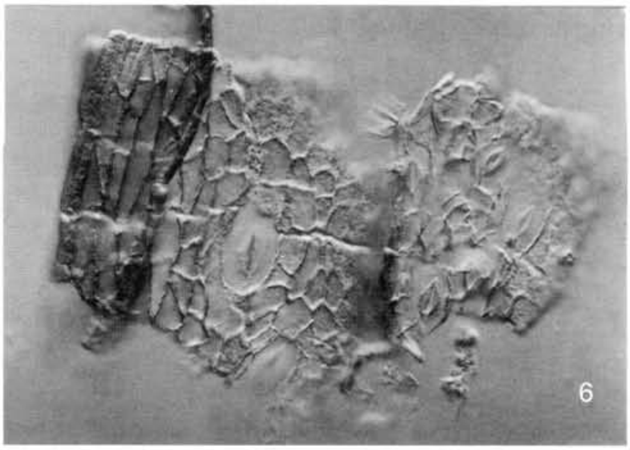
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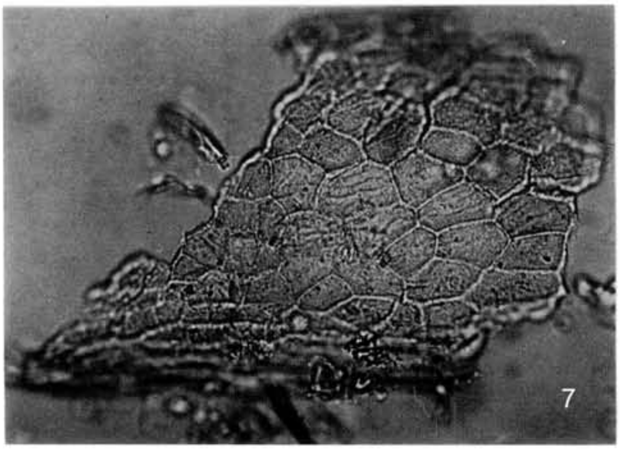
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Plate 5

Salix hausruckensis Kovar-Eder sp. nov.

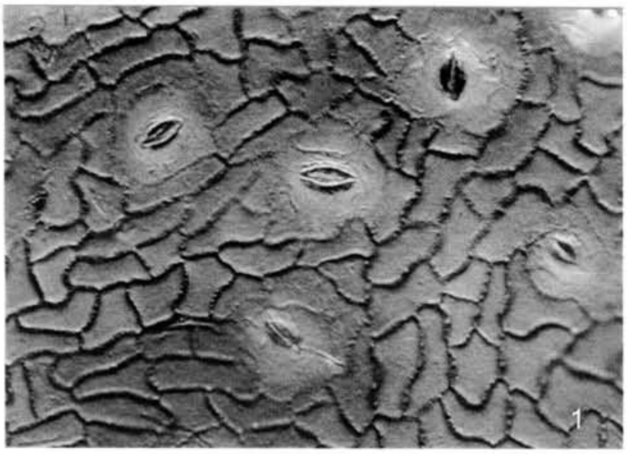
1, 2, 4, 6, 8. Abaxial cuticles

- 1, 2. Anticlines of non-modified epidermal cells exceptionally somewhat undulate, anticlines of the subsidiary cells not distinctly developed, trichome bases only scattered above veins, No. 1999B0043/203/1, 1. × 400
- 4. Paratype, anticlines of the subsidiary cells distinctly developed, trichome bases relatively dense on veins and in intercostal areas, No. 1999B0001/261/1
- 6. Paratype, trichome bases mainly upon veins, No. 1999B0043/408/2
- 8. Holotype, anticlines of the non-modified epidermal cells and subsidiary cells rather poorly developed, clearly visible only locally, trichome bases rare, even upon main veins, No. 1999B0001/9/1

3, 5, 7. Adaxial cuticle, anticlines straight, largely glabrous

- 3. Slight epicuticular striation upon vein, No. 1999B0043/203/1, × 400
- 5. Paratype, surface of non-modified epidermal cells often thickened, No. 1999B0043/408/2
- 7. Paratype, anticlines of the non-modified epidermal cells not distinctly developed, epicuticular striation locally well developed also in intercostal areas, No. 1999B0001/285/2

Unless otherwise stated × 200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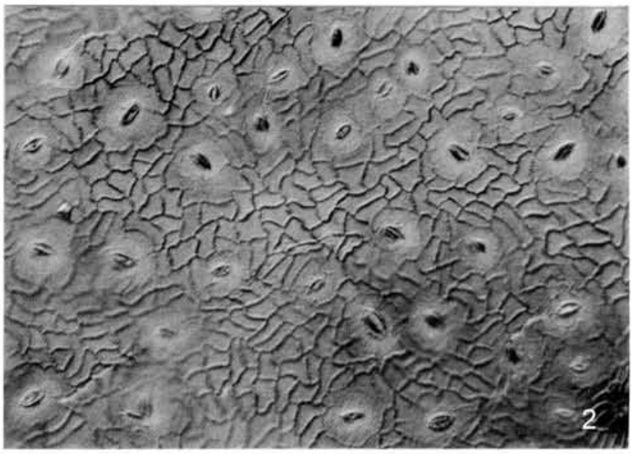
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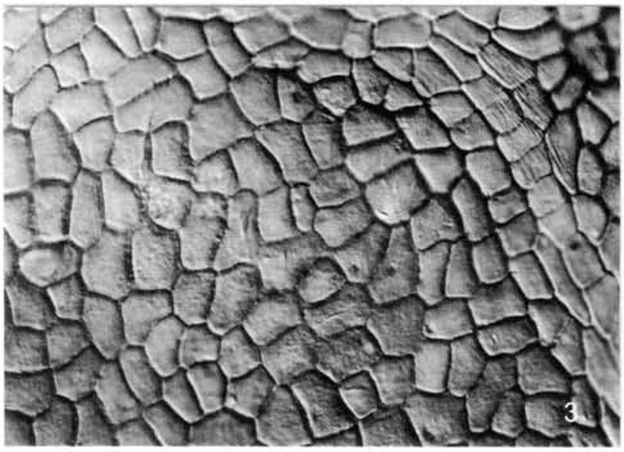
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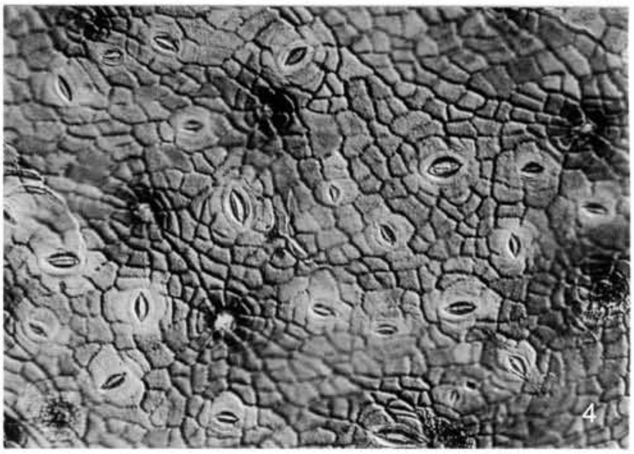
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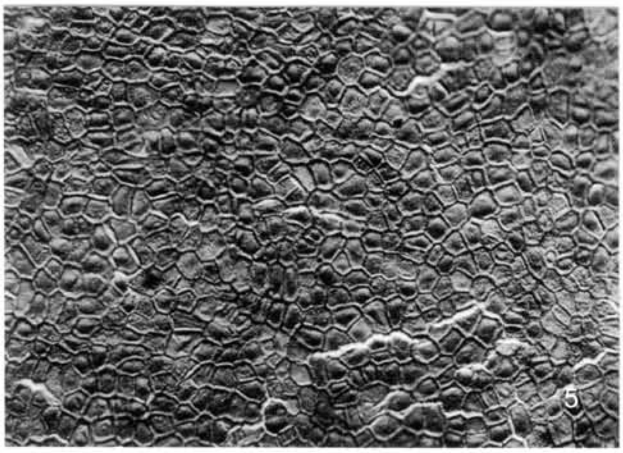
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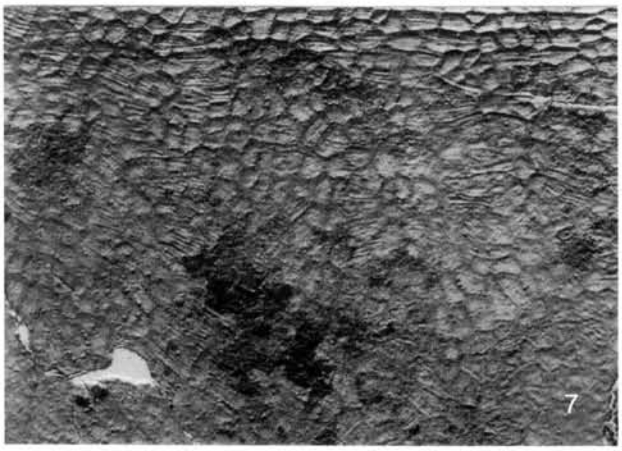
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Plate 6

Trapa ungeri Wójcicki & Kovar-Eder sp. nov.

1a, 1b. Paratype, No. 2000B0014/2

2. Holotype, No. 2000B0014/1

3–5. Paratypes
   3. No. 2000B0014/3
   4. No. 1988/0138/3 A, B
   5. No. 1988/0138/6

Trapa srodoniana Wójcicki

6. No. 1988/0138/1

Trapa ungeri Wójcicki & Kovar-Eder sp. nov. / *T. srodoniana* Wójcicki – putative hybrids

7. No. 1988/0138/2

8. No. 1988/0138/4

9. No. 1988/0138/5

Salix floridana Chapman

10. Cleared leaf prepared by D. Buechler, × 0.5

11. Apical petiolar glands on the upper leaf surface and lateral glanduliferous wings near the leaf base, × 5

Salix hausruckensis Kovar-Eder sp. nov.

12. Paratype, apical petiolar glands on the upper leaf surface near the leaf base, No. 1999B0001/23, × 5

Salix floridana Chapman

13. Abaxial cuticle, with brachyparacytic stomatal complexes and rare trichome bases, × 200

14. Adaxial cuticle with distinct epicuticular striation, × 400

Scale bar 1 cm


1a


2

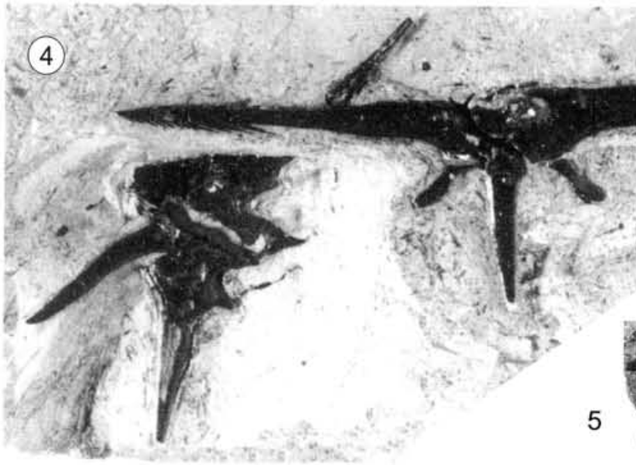

7


6


1b


3


8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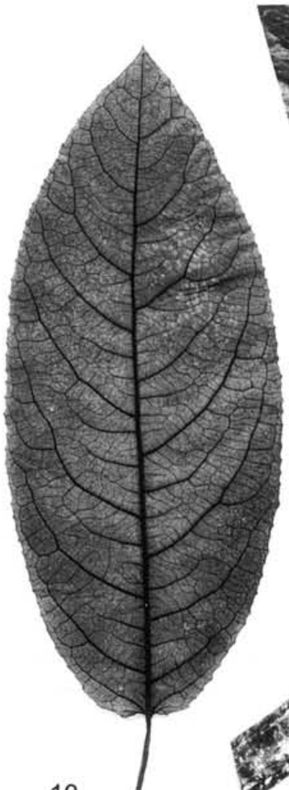
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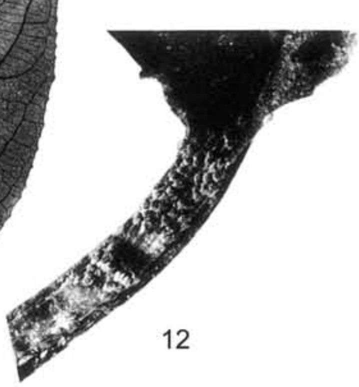
11


13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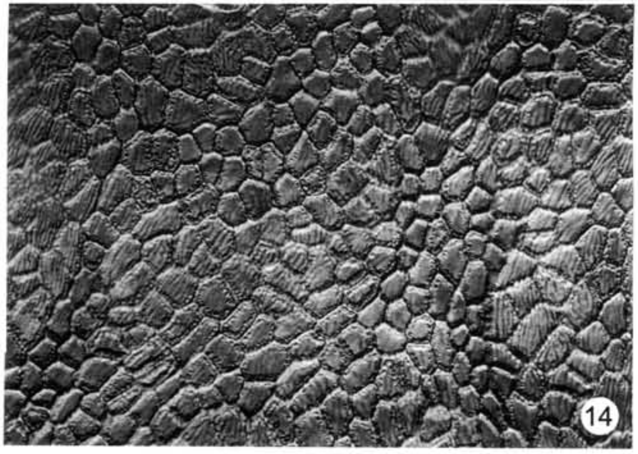
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