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The predominantly aquatic flora from Pellendorf, Lower Austria, Late Miocene, Pannonian – a systematic study

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ABSTRACT. The plant remains from a hydrophyte-bearing pelite of the sedimentary sequence at Pellendorf, Lower Austria (Miocene, Pannonian "zone" C) are investigated taxonomically. *Mikia pellendorfensis* Kovar-Eder & Wójcicki gen. et sp. nov. most probably represents floating leaves of a rooted aquatic plant. These leaves possibly belong to the plant that produced *Hemitrapa trapelloidea* Miki fruits. *Trapa pellendorfensis* Wójcicki & Kovar-Eder sp. nov. (fruits) co-occurs with *H. trapelloidea* even on the same bedding planes. The lower, approximately 2.7 m thick part of the investigated pelite is characterized by a mass-occurrence (monodominant) of *Decodon* leaves. In the upper approximately 1.1 m species are more diverse in aquatic plants: *Nitellopsis majoriformis* (Papp) Schwarz comb. nov., *Stephanochara* aff. *rochettiana* (Heer) Feist-Castel, *Ceratophyllum schrotzburgense* Hantke, *Ceratophyllum* sp. (fruits), Nymphaeaceae (rhizome fragments), *Hemitrapa trapelloidea*, *Trapa pellendorfensis*, *Mikia pellendorfensis*, and *Potamogeton* sp. (fruits) are documented there. The presented results here are fundamental for the palaeoecological interpretation of the whole sedimentary sequence at Pellendorf.

KEY WORDS: leaves, fruits, gyrogonites, taxonomy, new genus, new species, new combination, fossil flora, Pannonian, Miocene, Austria

INTRODUCTION

The flora studied derives from sections at the northwestern margin of the Vienna Basin. Their detailed description, the deduced palaeoecological development, and the stratigraphic implications are discussed in Harzhauser et al. (in press). We restrict ourselves here to unit 3 – the hydrophyte pelite, a pelite bearing a so far unique flora of prevalently aquatic plants. The Characeae have been investigated by J. Schwarz, the *Trapa* and *Hemitrapa* fruits by J.J. Wójcicki, whereas the palaeobotanical field studies and the investigation of the remaining taxa have been carried out by J. Kovar-Eder.

GEOGRAPHICAL AND GEOLOGICAL SETTING

Near Pellendorf (political district Mistelbach, Lower Austria, ÖK 1:50 000, Nos 24, 41) two gravel/sand pits are exploited: sand pit "Max" at latitude 48°30′00″N and longitude 16°32′08″E and gravel pit "Semrad" at latitude 48°29′54″N and longitude 16°32′12″E (Fig. 1). The sediment sequence there lies along the north-western margin of the Kronberg uplifted block, which is formed by the Bisamberg-fault

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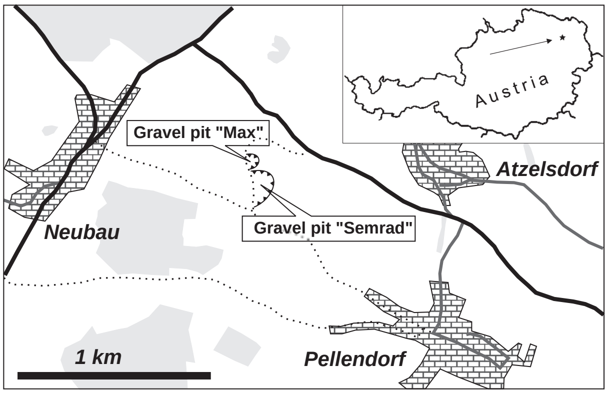

Fig. 1. Geographic location of the outcrops sand pit "Max" and gravel pit "Semrad" near Pellendorf, Lower Austria, Austria

zone. The composite sediment thickness measures 35 m and is divided into 5 units. The sequence documents a facial shift from riverine conditions (units 1 and 2, Hollabrunn-Mistelbach Formation) to freshwater marshes and lakes (unit 3 hydrophyte pelite), to near-coastal sands (unit 4), and finally offshore clays (unit 5) of "Lake Pannon". This facies succession is more likely linked to eustatic changes at the north-western margin of the Vienna Basin than to local changes in the riverine system. Biostratigraphically the sequence corresponds to the Pannonian "zone" C sensu Papp (1951b, 1953, see also Harzhauser et al. in press).

Unit 3 – the hydrophyte pelite (bearing the here-described flora) – is well developed in the sand pit "Max" (up to 5 m thick, Fig. 2) and to a lesser extent in the gravel pit "Semrad". It follows the sandy unit 2, which lacks plant remains, and it is topped by the sandy/silty unit 4, which bears only occasional, single, poorly preserved leaf fragments. For the detailed sedimentological, palaeoecological, and stratigraphic investigations of the entire sequence we refer to Harzhauser et al. (in press).

MATERIAL AND PRESERVATION

Most of the plant material (leaves and fruits) is preserved as oxidized imprints of very low contrast only. The gyrogonites are calcified. In the upper part of the hydrophyte pelite especially floating leaves and *Ceratophyllum* shoots are covered by a turgescent Ca-rich layer. The latter preserves even the surface of the epidermis cells as it has already been described from *Potamogeton* fossils from Wörth and Reith, Styrian Basin, Pannonian (Kovar-Eder & Krainer 1990, 1991). From washed samples, only a few carbonised but poorly preserved fruits (*Potamogeton*) were obtained. All material is kept in the palaeobotanical collection of the Naturhistorisches Museum Wien. The collection file Nos correspond to the different levels from which the material was collected (Tab. 1).

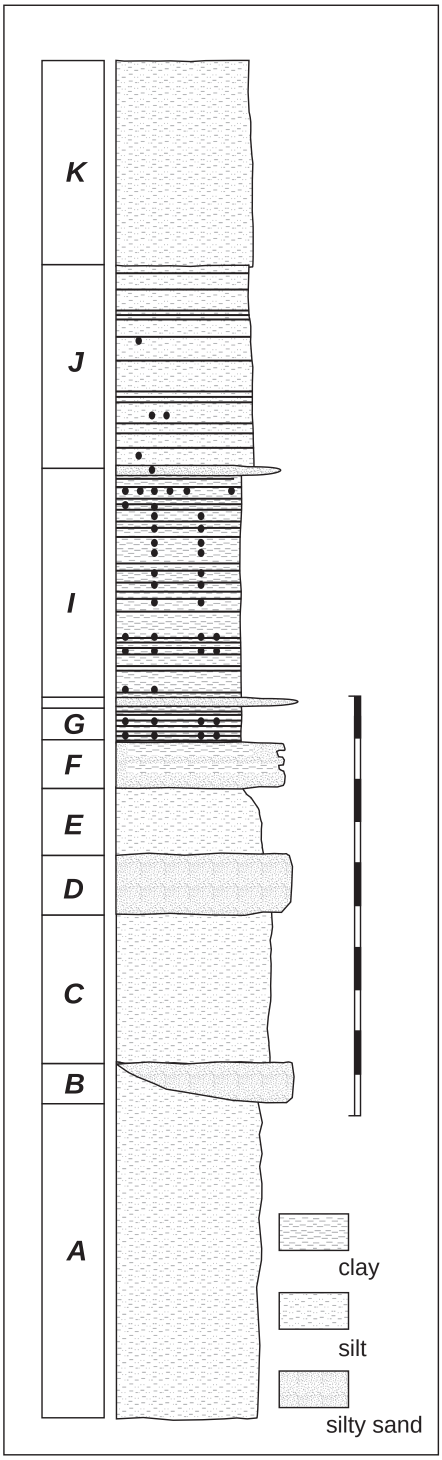

Fig. 2. Profile through the hydrophyte pelite (unit 3 in Harzhauser et al. in press). **A, C, E, G** – mass-occurrence of *Decodon* sp.; **I, J** – higher diversity of aquatic plants (*Trapa pellendorfensis*, *Hemitrapa trapelloidea*, Nymphaeaceae, *Ceratophyllum schrotzburgense*, and others, but less rich in *Decodon* (compare Tab. 3). Scale bar 1 m

Table 1. Material collected from different subunits of the hydrophyte pelite and their corresponding coll. file nos

Position in the hydrophyte pelite	Subunit	Coll. file nos
Section sand pit "Max" (from bottom to top)		
1.5–1.6 m	A	2000B0006/, 2000B0007/
0.1 m	B	2000B0005/
0.4 m	C	2000B0002/,2000B0003/, 2000B0004/
0.1 m	G	2000B0010/
0.8 m	I	2000B0009/
0.5 m	J	2000B0008/
From the upper part of the hydrophyte pelite but not *in situ*		1999B0056/, 2000B0011/, 2000B0029/
Loose material, position in the section unclear		1999B0051/
Section gravel pit "Semrad"		
Hydrophyte pelite, probably upper part		1997B0019/

SYSTEMATIC DESCRIPTION

Characeae

The two samples investigated here derive one each from the subunits I and J.

Nitellopsis majoriformis (Papp) Schwarz **comb. nov.**

Pl. 1, figs 11–16, 21

1951a *Chara majoriformis* sp. nov.; Papp, p. 282, Pl. 1, fig. 1.
1954 *Chara majoriformis* Papp; Horn af Rantzien, p. 25.
1955 *Tectochara majoriformis* (Papp) Mädler; Mädler, p. 298.
1959 *Tectochara majoriformis* (Papp) Mädler; Horn af Rantzien, p. 80.
1979 *Tectochara majoriformis* (Papp) Mädler; Mädler & Staesche, p. 106, Pl. 7, figs 6–9.

Basionym. *Chara majoriformis* Papp, Sitzungsber. Österr. Akad. Wiss., math.-naturwiss. Kl., Abt. I, 160: 282, Pl. 1, fig. 1. 1951.

Material. Coll. file Nos 2000B0008/53 (100 specimens); 2000B0009/38 (ca. 460 specimens).

Description. Mature gyrogonites ovoid to rounded ovoid, very rarely nearly globular in shape, immature specimens distinctly more slender; apex not protruding, usually well rounded; base normally slightly narrowed and truncate at the end, only exceptionally rounded; basal pore situated at the centre of a basal funnel; the funnel pentagonal (87% of the measured specimens) or slightly bowl-shaped (13%); this corresponds well to types 2 and 3 of the basal pore morphology of *Nitellopsis* (Soulié-Märsche 1975); in mature specimens spiral cells mostly distinctly convex with smooth surface (lacking irregular thickenings), only exceptionally slightly convex or almost flat, in immature specimens flat to concave; periapically the spiral cells are always clearly constricted and depressed, while their apical ends are widened and thickened again, bearing distinct apical nodes in most of the mature specimens.

Measurements of 100 specimens from subunit I (coll. file No. 2000B0009/38), mean values in brackets "( )": length of gyrogonite 1030–1410 µm (1225–1325 µm), width of gyrogonite 930–1280 µm (1100–1200 µm), isopolarity index (length × 100/width) 102–121 (105–115), width of spiral cells 150–200 µm (170–190 µm), number of convolutions 8–10 (9), spirality coefficient (length of gyrogonite/width of spiral cells) 5.6–8.4 (6.8–7.4), diameter of basal pore 40–110 µm (60 µm).

Remarks. The gyrogonites from subunit I (coll. file No. 2000B0009/38) represent mostly mature specimens, while those from subunit J (coll. file No. 2000B0008/53) are characteristically immature forms.

The decisive factors to group the gyrogonites from Pellendorf to the subgenus *Tectochara* of the genus *Nitellopsis* are their ovoid shape, the slightly narrowed basal region and the distinct basal funnel (Grambast & Soulié-Märsche 1972).

Due to their general appearance, the gyrogonites studied here are part of the *Nitellopsis meriani* (Braun ex Unger) Grambast & Soulié-Märsche "species-complex", which includes, besides the type species, morphologically more or less well-distinguishable morphotypes or species such as *N. globula* (Mädler) Grambast & Soulié-Märsche, *N. helvetica* (Mädler) Grambast & Soulié-Märsche and *N. huangi* (Lu) Grambast & Soulié-Märsche. Within this complex the gyrogonites dealt with here correspond to the type species *N. meriani*.

Considering the extreme values of the measured parameters (length, width, etc.), those of the described material clearly match or even exceed the upper size classes of *N. meriani*. Variation statistics (Fig. 3) reveal marked differences between the Pellendorf material and "typical" populations of *N. meriani*, originating from different sites and different stratigraphic ages (e.g. Schwarz 1985, 1988, Soulié-Märsche et al. 1997). The gyrogonites described here, however, are characterized by invariably bigger size, more globular shape, much wider spiral cells and fewer convolutions. This is especially evident comparing the size classes of the highest percentage (Tab. 2). Thus, these differences require the separation of the gyrogonites dealt with here from *N. meriani* and the assignment to *Nitellopsis majoriformis* (Papp) Schwarz comb. nov., originally described by Papp (1951a) as *Chara majoriformis*, transfered later by Mädler (1955) to the genus *Tectochara*. The required new combination is validated above. The new combination is necessary because, according to Grambast & Soulié-Märsche (1972), *Tectochara* represents presently only a subgenus of *Nitellopsis*,

Although only two specimens were available to Papp (1951a), he already clearly recognized the diagnostic characters to distinguish them from *Nitellopsis* (former *Chara*) *meriani* and established *Chara majoriformis*. Later, rich material was available only to Mädler and

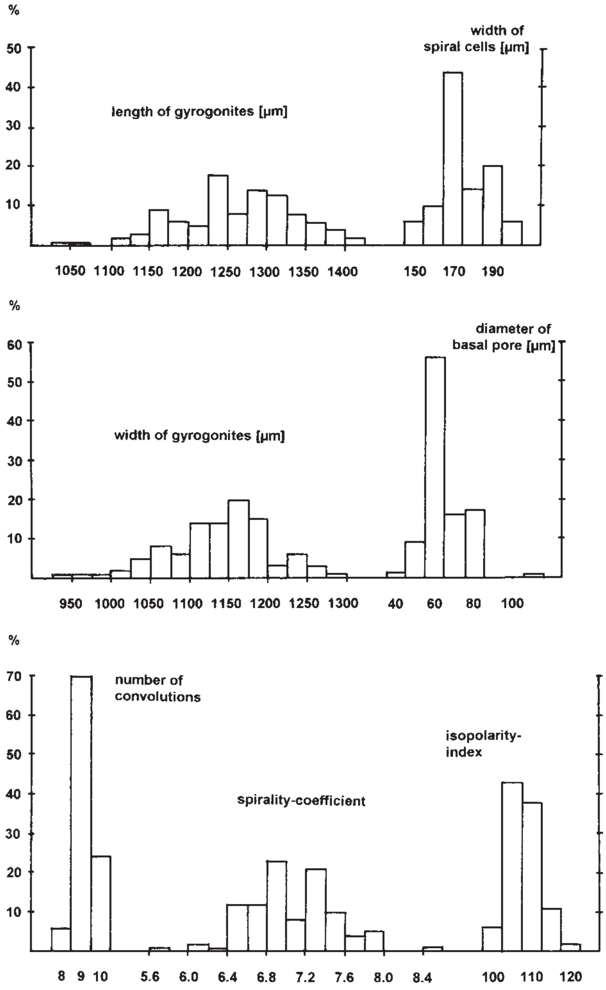

Fig. 3. Histograms of some parameters of *Nitellopsis majoriformis* (Papp) Schwarz comb. nov., coll. file No. 2000B0009/38; n=100 gyrogonites

Table 2. Comparison of some important parameters *of Nitellopsis majoriformis* (Papp) Schwarz comb. nov. and *N. meriani* (Braun ex Unger) Grambast & Soulié-Märsche. For each parameter the size classes with the highest percentage are given; extreme values in ( )

Species Character	*Nitellopsis majoriformis* (100 specimens) Upper Miocene Pellendorf (this publication)	*Nitellopsis meriani* (ca. 200 specimens) Oligocene / Lower Miocene Mainz Basin (Schwarz 1985)	*Nitellopsis meriani* (800 specimens) Oligocene Mainz Basin (Schwarz 1988)	*Nitellopsis meriani* (100 specimens) Middle Miocene Thailand (Soulié-Märsche et al. 1997)
Length of gyrogonites (µm)	(1030) 1225–1325 (1410)	(840) 1150–1250 (1410)	(860) 1050–1225 (1370)	(900) 1075–1225 (1275)
Width of gyrogonites (µm)	(930) 1100–1200 (1280)	(690) 950–1050) (1160)	(680) 900–1000 (1160)	(700) 900–1000 (1100)
Isopolarity index	(102) 105–115 (121)	(105) 115–125 (145)	(103) 110–125 (142)	(105) 115–130 (145)
Width of spiral cells (µm)	(150) 170–190 (200)	(90) 130–150 (190)	(90) 130–150 (170)	–
Number of convolutions	(8) 9 (10)	(9) 10–11 (12)	(9) 10–11 (12)	–

Staesche (1979), enabling them to give an emended diagnosis. Their characterization of *Tectochara majoriformis* “Die Eigenschaften von *Tectochara meriani* sind hier ins Extrem gesteigert” (ibid. p. 107) matches very well the Pellendorf material.

Stephanochara aff. ***rochettiana*** (Heer) Feist-Castel

Pl. 1, figs 17–19

1854 *Chara rochettiana* Heer n. sp.; Heer, p. 26, Pl. 4, fig. 9 a, b.
1955 *Tectochara rochettiana* (Heer) Mädler; Mädler, p. 287, Pl. 25, figs 8–11.
1959 *Croftiella rochettiana* (Heer) Mädler; Horn af Rantzien, p.105.
1977 *Stephanochara rochettiana* (Heer) Feist-Castel; Feist-Castel, p. 124.

Material. Coll. file No. 2000B0008/52: 12 gyrogonites, 7 of them complete.

Description. Gyrogonites ovoid to ellipsoid; apex as a rule very strongly flattened, rarely slightly protruding in the centre; basal region narrowed and truncate at the end; basal pore in most cases situated at the bottom of a small but distinct basal funnel; spiral cells usually somewhat convex, rarely flat, surface smooth; periapically the spiral cells are markedly narrowed and reduced in thickness, always becoming concave, but there are no depressions; the apical ends are noticeably widened and somewhat thickened, but lack distinct apical nodes.

Measurements: length of gyrogonite 850–990 µm, width of gyrogonite 620–700 µm, isopolarity index (length × 100/width) 124–143, width of spiral cells 80–110 µm, number of convolutions 10–12, diameter of basal pore 30–50 µm.

Remarks. At first sight, the slender shape of the gyrogonites and the flat apical region resemble *Rantzieniella nitida* Grambast and *Lamprothamnium* species. The former, however, differs by a more distinct cylindrical shape, a well-rounded base, wider spiral cells, and an “operculum” formed by the apical ends of the spiral cells (Grambast 1962, Soulié-Märsche 1989: Pl. 13, figs 4–5).

Also in *Lamprothamnium*, the gyrogonites are more cylindrical with a rounded base. The apex is even more distinctly flattened, very often depressed. It is usually only poorly calcified and therefore often not preserved, e.g. in the modern *Lamprothamnium papulosum* (Wallroth) J.Groves (Mojon 1989, Soulié-Märsche 1989, 1998), and in the fossil *L. priscum* Castel & Grambast. In contrast, the gyrogonites from Pellendorf bear terminally thickened spiral cells apically. Moreover, they lack the fan- or Y-shaped calcification mode which is characteristic of *Lamprothamnium*.

Based on the apical and periapical morphology, the material described here matches best with the genus *Stephanochara*. Due to the convex spiral cells there is a very strong resemblance to the closely related species *S. ungeri* Feist-Castel and *S. rochettiana* (Heer) Feist-Castel. According to Mädler (1955) and Berger (1983), *S. rochettiana* is distinguished from *S. ungeri* (former *Chara escheri* A. Braun ex Unger) by more slender gyrogonites, narrower spiral cells, a higher number of convolutions, and only faintly developed apical nodes. In these characters as well as in their size, the specimens from Pellendorf correspond quite well with *S. rochettiana*. In this species, however, the base of the gyrogonites is mostly well-rounded and the apex is less flat (compare Mädler 1955: Pl. 25, figs 8–11 and Berger 1983: Pl. 2, figs 2–4 – paratypes). Therefore, we restrict ourselves to the “affine” determination.

Cupressaceae

Taxodium dubium (Sternberg) Heer

Pl. 3, fig. 10

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

Material. Coll. file Nos 1997B0019/1, 4–40, 43, 44 (twigs), 2, 3, 41, 50 (isolated cone scales); 45–49 (*Taxodium dubium* vel *Sequoia abietina*).

Description. Mainly terminal shoots gradually tapering towards the base and the apex; needles slender, straight or slightly curved outwards, spirally inserted, but distichously (taxodioid) arranged along the axes, needle base decurrent, apex acute.

Remarks. The *Taxodium* shoots were found restricted to one layer exposed only regionally in the western part of the gravel pit “Semrad”. There, the shoots are abundant and monodominant. This exposure possibly corresponds to the hydrophyte pelite. Isolated cone scales were found associated. Some remains have broader needles, so the presence of *Sequoia abietina* (Brongn.) Knobloch cannot be ruled out completely.

Nymphaeaceae

Nymphaeaceae gen. et sp. indet.

Pl. 4, fig. 5a,b

Material. Coll. file Nos 2000B0008/10, 12, 19, 20, 22=48 (counterpart), 24, 30=44 (counterpart), 33, 34; 2000B0029/23, 24, 42, 46, 50, 51.

Description. Imprints of rhizome fragments, straight to slightly curved, equally slender, up to 180 mm long, 10–15 mm wide; leaf scars rounded, consistent diameters of the leaf scars (3–)4–5(–6) mm; central air channel (?) present; scars of roots only rarely distinct.

Discussion. According to the recent investigations (Gee pers. comm.), the leaf scar pattern (rounded leaf scars) of these rhizomes points towards *Nymphaea*. The rhizomes are restricted to the subunits I and J of the hydrophyte pelite embedded parallel to the bedding there.

Ceratophyllaceae

Ceratophyllum schrotzburgense Hantke

Pl. 4, figs 1–4

1954 *Ceratophyllum schrotzburgense* Hantke; Hantke, p. 71, Pl. 11, figs 9–13.

Material. Coll. file Nos 2000B0008/5, 6=14 (counterpart), 13, 15, 17, 18, 28, 35–37=50 (counterpart), 43, 48, 49; 2000B0009/13, 18, 23, 28, 33, 34, 36.

Description. Shoots with whorls of dichotomously forking leaves, isolated leaves and their fragments, linear up to 1.5 mm wide before dichotomously forking, leaves tapering apically; leaf margin smooth especially in the lower leaf parts, but in some cases distinctly brittle in apical leaf parts; remains preserved as (iron-coloured) oxidised imprints covered by a hyaline, Ca-rich layer showing the turgescent surface cell-structure already at relatively low magnification (20×). Straight-walled, tetra-, penta-, hexagonal cells arranged in straight and parallel rows.

Remarks. The type specimens of *Ceratophyllum voesendorfense* are probably lost, and in any case were not available for reinvestigation. Its leaves have been described by Berger (1952) as lacking marginal teeth, contrary to modern *Ceratophyllum* species. The remains described as *C. tertiarium* by Ettingshausen (1888, 1890) are not similar to our material, whereas *C. schrotzburgense* from Schrotzburg matches quite well.

Ceratophyllum sp.

Pl. 3, figs 11–13

Material. Coll. file Nos 2000B0029/4 A, B, 5, 6 A–C, 7–12 A, 17, 18.

Description. Fruit imprints only, shape of fruit body oval, 4–5 mm long, 3–4 mm wide, in several specimens two basal slender spurs developed, incompletely (up to 5 mm long) preserved, apically an up to 8 mm long spur (style) developed. Marginally running furrows on both sides indicate the venation course.

Remarks. Species lacking a distinct style and/or basal spurs can be excluded, e.g. *Ceratophyllum miocenicum* Dorof., *C. lusaticum* Mai, *C. dubium* (Ludwig) Kirchh. However, the preserved features are insufficient for a reliable specific determination. Most probably these achenes derive from the vegetative shoots of *C. schrotzburgense*.

Ulmaceae

Ulmus carpinoides Goeppert emend. Menzel

Pl. 3, fig. 9

1855 *Ulmus carpinoides* Goepp.; Goeppert, p. 28, Pl. 13, figs 4–9.
1906 *Ulmus carpinoides* Goepp.; Menzel, p. 67, Pl. 4, figs 5, 6, 9–16.

Material. Coll. file No. 2000B0008/39.

Description. Lamina elliptic, 56 mm (when complete about 60 mm) long, 25 mm wide, slightly asymmetrical, base incomplete, apex acute/acuminate, margin double serrate, midvein almost straight, secondaries simple craspedodromous, numerous and densely spaced, maximal distance between secondaries 5 mm (more commonly about 3 mm distance), arising at angles of max. 45° to approximately 20° in the apical leaf part, entering in a slight curve the first order teeth, ending in their apices; from the secondaries, next order veins arise towards basal and enter marginal teeth; higher order venation poorly preserved.

Remarks. Many authors still treat *Ulmus carpinoides* and *U. pyramidalis* Goeppert as separate species. Following Menzel's opinion, we refer here to the discussion in Kovar-Eder (1988).

Salicaceae

Populus L.

Among the very numerous Miocene localities in Austria, *Populus* is diversely represented only in Pellendorf (Akhmetiev & Kovar-Eder pers. comm.).

Populus balsamoides Goeppert

Fig. 6: 2

1855 *Populus balsamoides* Goepp.; Goeppert, p. 23, Pl. 15, figs 5, 6.

Material. Coll. file Nos 1997B0019/53; 2000B0009/2, 11.

Description. Poorly preserved leaf fragments, petiole straight up to 65 mm long (still incomplete), lamina triangular, up to 85 mm long (incomplete), width up to at least 80 mm; leaf base slightly cordate; midvein straight, secondaries originating in distances of 10–20 mm, curved, tertiaries forked percurrent, oblique, higher order venation reticulate, margin and leaf apex not preserved.

Only specimen No. 2000B0009/2 (Fig. 6: 2) is an almost complete, small leaf: petiole 17 mm long, length of lamina 47 mm, width 40 mm, lamina almost elliptic, base rounded, apex acuminate?, leaf margin serrate, basal and apical sides of the teeth convex, tooth apex rounded with occasionally preserved gland imprints, midvein slightly wavy, secondaries semicraspedodromous, forming marginal loops, higher order veins also forming loops along the margin, terminal veins running into the tooth apex, tertiaries forked percurrent, oblique.

Remarks. Although rare and poorly preserved, there is no doubt about the presence of this species.

Populus mutabilis Heer

Fig. 6: 1

1856 *Populus mutabilis* Heer; Heer, p.19, Pl. 60, figs. 12 b, Pl. 61 (excl. figs 5,12, 14), Pl. 63, figs 1–4.

Material. Coll. file Nos 2000B0004/25; 2000B0009/5; 2000B0029/2, 3 A–C.

Description. Petiole up to 22 mm long; lamina triangular to ovate, length up to 135 mm, width up to 70 mm but probably even > 80 mm, relation length/width 1.3–1.7, base slightly cordate or rounded, margin entire, midvein straight, in one specimen slightly curved, secondaries arising in distances of 13–22 mm, first pair of secondaries arising almost at the base, in one leaf running parallel on the basal leaf margin, secondaries slightly curved, brochidodromous, tertiaries forked percurrent.

Remarks. These leaves correspond very well with the entire-margined leaves of *Populus mutabilis*. The material from Pellendorf contains no specimens with few or irregular teeth as described by Heer (1856).

Populus populina (Brongniart) Knobloch

Fig. 6: 3

1822 *Phyllites populina* Brongn.; Brongniart, p. 237, Pl. 14, fig. 4.
1964 *Populus populina* (Brongn.) Knobloch comb. nov.; Knobloch, p. 601.

Material. Coll. file Nos 1999B0051/0002; 2000B0007/5,6,7; 2000B0029/1; ? 1997B0019/55.

Description. Leaves triangular, petiole up to 32 mm long, leaf base truncate, slightly cordate, length of lamina up to 50 mm (when complete about 65 mm), width up to 70 mm, leaf margin simple serrate, teeth slightly hooked, secondaries arise in irregular distances of 2–16 mm from the midvein, course of the midvein and secondaries slightly wavy (to zigzag), secondaries occasionally forked, running slightly curved and among each other diverging towards the margin, secondaries semicraspedodromous, marginal ultimate venation looped/incomplete, tertiaries forked percurrent, higher order venation reticulate.

Remarks. The morphological characteristics allow a clear differentiation between *Populus balsamoides* and *P. populina*.

Trapaceae

This is the first evidence of a co-occurrence of *Trapa* L. and *Hemitrapa* as defined by Miki (1941) in the Neogene. The other two reports seem doubtful: *Hemitrapa pseudoborealis* Budantzev (1960) from Tertiary sediments around Lake Baikal, associated with *Trapa* there, is probably a misinterpretation of the fossil fruit figured as holotype (see also Gregor 1982). In fact, it is the fruit compression along the plane of the lower horns that probably represents one of the three *Trapa* species described in this paper. Unfortunately, the material was not available during the visit of JJW to the palaeobotanical collection of LE. Also, *Hemitrapa heissigii* Gregor from the Zennern Depression near Fritzlar (Germany, Miocene?/Pliocene; Huckriede & Urban 1998) should rather be placed in the genus *Trapa*. Additionally, spines with harpoons – as figured in this paper and reckoned to belong to *Hemitrapa* – are characteristic of *Trapa:* those of *Hemitrapa* are much more finely and densely barbed.

Hemitrapa trapelloidea Miki

Fig. 4, Pl. 2, figs 1–12

?1933 *Trapa teumerii* Menzel. sp. nov.; Menzel, p. 26–27, Pl. 7, figs 2 a-g.
1941 *Hemitrapa trapelloidea* Miki gen. et sp. nov.; Miki, p. 289, Fig. 19 D, Pl. 7 D.
1952 *Hemitrapa trapelloidea* Miki; Miki, p. 347–350, Fig. 1, 2 E.
1959 *Hemitrapa trapelloidea* Miki; Miki, p. 291, Fig. 2 A, 3 B.
?1960 *Trapa vassiljevii* Kornil. sp. nov.; Kornilova, p. 67–69, Pl. 11, figs 1–9, Pl. 28, figs 7–10.
?1961 *Hemitrapa borealis* (Heer) Miki; Tanai, p. 382–383, Pl. 32, figs 6, 7.
?1963 *Hemitrapa borealis* (Heer) Miki; Tanai & Suzuki, p. 145, Pl. 10, figs 18, 19.
?2001 *Hemitrapa teumerii* (Menzel) Budantzev; Mai, p. 111–112.

Material. Coll. file Nos 2000B0008/1, 4, 9, 22A, B = 48, 26, 27, 29, 31, 38, 45, 47A, B; 2000B0009/15; 2000B0029/19–32.

Description. Imprints of fruits mostly (12–16)19–34 mm high including conically-pointing apical bristles up to 6 mm long, fruit base mostly acute, rarely somewhat rounded in outline, always with adhering peduncle fragments of up to 10 mm length; fruit with well-defined head, 4–8 mm high, usually abruptly narrowed into a 3–6 mm long, conical to subconical neck; surface of fruit head and neck finely ribbed; frame of fruit usually well pronounced, with two pairs of upward-pointing to ascending (50°–85°) slender arms, inserted above the center of the fruit body, arms up to 0.7 mm wide and 10–18 mm long, armed apically with 10–15 mm long, retrorsely barbed harpoons, arms slightly broadened at the base; one pair of arms probably somewhat shorter and inserted slightly below the line joining the bases of longer arms; additional reduced arms on the fruit frame between long arms very probable; the fruits are broadest (10–15 mm) in the line of their frame; surface of the lower part of the fruit body, on one side only, covered with at least five protruding longitudinal ribs.

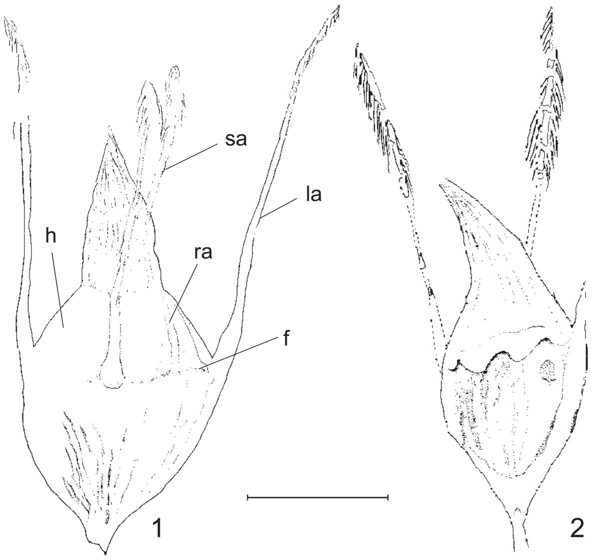

Fig. 4. *Hemitrapa trapelloidea* Miki. **f** – frame, **h** – head of fruit, **la** – longer arm, **ra** – probable imprint of reduced additional arm, **sa** – shorter arm. 1 – No. 2000B0008/1; 2 – No. 2000B0009/15. Scale bar 1 cm

Discussion. These fruit imprints from Pellendorf (Fig. 4; Pl. 2, figs 1–12) represent typical *Hemitrapa trapelloidea* specimens as described and figured by Miki (1941, 1952, 1959) from the Neogene of Japan. This species is distinct amongst other known *Hemitrapa* species in its characteristic fruit shape and its long, very slender arms inserted above the center of the fruit body. Similarly to the Japanese material, the fruits from Pellendorf possess one pair of longer and one pair of at least slightly shorter arms. The latter are inserted somewhat below the former (Fig. 4: 1, Pl. 2, fig. 1). As the pairs of lower and upper arms differ only slightly in length it is usually difficult to determine precisely the compression plane. The compression either along the plane of the upper (longer) or lower (shorter) arms may explain the variability in fruit width and neck shape as known from Japanese *Hemitrapa* fruits: they are slightly wider along the plane of the longer arms than along that of the shorter ones. When compressed along the plane of the shorter arms, the neck attenuates more gently into the fruit head (Pl. 2, figs 14–15; see also Miki 1941, 1952, 1959). Additionally, in some specimens from Pellendorf (e.g., specimens coll. Nos 2000B0008/1, 2000B0029/20, 28) faint traces between the long arms are discernable on the fruit frame, suggesting the presence of additional reduced arms characteristic of *H. trapelloidea* (similar structures but reduced to tubercles of different size and shape are present in *Trapa*).

Hemitrapa trapelloidea differs from the two *Hemitrapa* species known from the European Palaeogene/Neogene, i.e. *Hemitrapa pomelii* (Saporta) Mai reported from the late Oligocene of France (Saporta 1878, Boulay 1899) and early Miocene of Germany (Mai & Walther 1991), and *H. heissigii* Gregor (Gregor 1982, Wójcicki & Kvaček 2002). The first is recognized mainly by the relatively narrowly oblong-elliptical outline of its fruits and by slender arms located more closely to the fruit base. The fruits of *H. heissigii*, on the other hand, have solid ascending horns with relatively thick bases. In addition, some morphotypes included into this species possess at least small tubercles between the upper and lower horns. *Hemitrapa heissigii* as originally defined by Gregor (1982), along with morphotypes included here recently by Mai (2001), seems to be heterogeneous and needs further detailed studies.

Most probably, the fruits reported from Japan by Tanai (1961) and Tanai and Suzuki (1963) and determined as *Hemitrapa borealis* (Heer) Miki represent *H. trapelloidea*. At the same time, note that the Japanese localities are Miocene in age; this includes the *H. trapelloidea* type material from the Seto Porcelain Clay Formation that Miki (1941) reported to be of Pliocene age (cf. Tsukagoshi et al. 1995, Momohara 1997, Tsukagoshi 2000).

Judging from the protologue of *Trapa vassiljevii* (Kornilova 1960; Kazakhstan, Early Miocene), these fossil fruits should clearly rather be placed in *H. trapelloidea*. Moreover, morphological evidence points to *Hemitrapa teumerii* (Menzel) Budantzev (Menzel 1933, Germany, middle Miocene) also being conspecific with *H. trapelloidea* (cf. Gregor 1982). Problems with identifying *Hemitrapa* fruits as well as the status of the genus and its systematic position are, however, the subject of ongoing investigations.

Trapa pellendorfensis Wójcicki & Kovar-Eder, **sp. nov.**

Fig. 5: 1–6, Pl. 1, figs 1–10

Holotype. Naturhistorisches Museum, Geologisch-Paläontologische Abteilung, Coll. file No. 2000B0009/3 (Fig. 5: 1, Pl. 1, fig. 1).

Paratypes. Naturhistorisches Museum, Geologisch-Paläontologische Abteilung, Coll. file Nos 2000B0008/23 A–F (Fig. 5: 2, 3, 5, Pl. 1, figs 4–6), 2000B0029/33 (Fig. 5: 4, Pl. 1, fig. 9), 34 A–C (Fig. 5: 6, Pl. 1, fig. 2, 3, 10); 35 (Pl. 1, fig. 7); 36 (Pl. 1, fig. 8).

Further material. Coll. file Nos 2000 B0009/22, 31A,B, 34.

Type locality. Pellendorf, Lower Austria, Austria.

Type horizon. Clays representing marginal facies of Lake Pannon (unit 3 – hydrophyte pelite according to Harzhauser et al. in press).

Age. Miocene, Pannonian “zone” C sensu Papp (1951a, 1953).

Derivation of the name. The specific epithet refers to Pellendorf, a village near the *locus classicus* of the species.

Description. Imprints of small fruits, obtriangular in outline, with four horns; fruit 7–12 mm high (including neck), width at the level of the upper horns 15–23 mm; fruit about 1.9–2.7 times as wide as high; fruit head pronounced, 4–6 mm long, its upper end bearing a well-developed straight cylindrical neck; neck 1.2–2.0 mm long and 1.5–2.0 mm broad, corona lacking; apical aperture with a ring of upward-pointing hairs; surface of fruit head and neck finely ribbed; upper horns solid, 5–9 mm long, narrowly triangular in outline, gradually attenuated into straight elongate, thin, spine-like tips, widely spread or ascending (50°-80°), probably with a smooth surface except for the at least 5 mm long, retrorsely barbed spines (harpoons), base of the upper horns attenuate gently into the upper surface of the fruit or sometimes slightly raised at the base; no mat areas present at the base and/or apical part of the upper horns; lower horns at least slightly retrorse, straight, relatively narrow, not less than 4 mm long, inserted (1/4) 1/3 (2/5?) from the fruit’s base; fruit frame well developed; on the fruit frame between the bases of the upper and lower horns, small tubercles are developed, at least up to 0.3 mm long; lower part

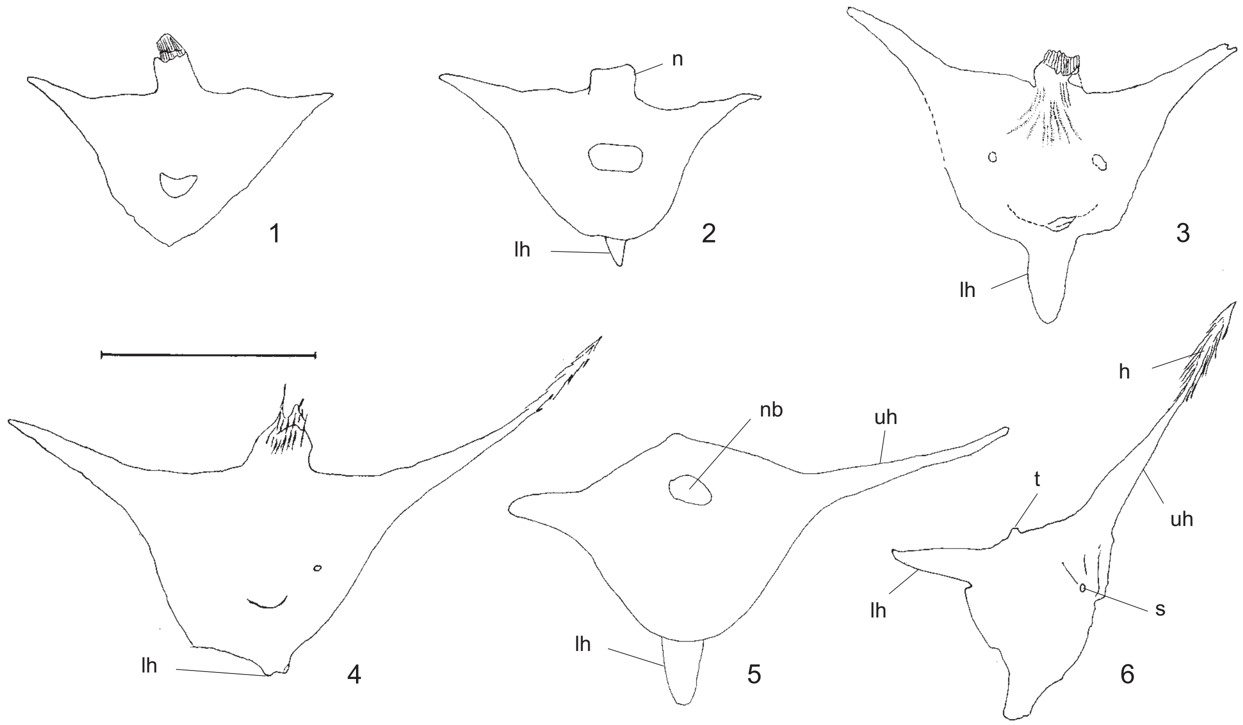

Fig. 5. *Trapa pellendorfensis* Wójcicki & Kovar-Eder, sp. nov. **h** – harpoon, **lh** – lower horn, **n** – neck, **nb** – neck base, **s** – scar, **t** – tubercle, **uh** – upper horn. **1** – Holotype. No. 2000B0009/3 (=Pl. 1, fig. 1); **2–6** – Paratypes. 2 – No. 2000B0008/23 C (=Pl. 1, fig. 4), 3 – No. 2000B0008/23 A (=Pl. 1, fig 6), 4 – No. 2000B0029/33 (=Pl. 1, fig. 9), 5 – No. 2000B0008/23 B (=Pl. 1, fig. 5), 6 – No. 2000B0029/34 B (=Pl. 1, fig. 10). Scale bar 1 cm

of the fruit body regularly obtriangular in outline, with slightly to distinctly rounded base (no peduncle adherent), its surface, on one side only, covered with at least three protruding longitudinal ribs; basal ring not visible; basal scar small, probably at least 0.3 mm in diameter.

Discussion. Relatively abundant material and different positions of the fruits in the sediment enabled detailed characterization of *Trapa pellendorfensis*. The fruits of the newly described species possess well-developed, relatively narrow lower horns (Fig. 5: 2–6, Pl. 1, figs 1–10) and small tubercles between the upper and lower horns (Fig. 5: 3, 4, 6, Pl. 1, fig. 10).

This new conspicuous species differs significantly from known extant and fossil ones (see Wójcicki et al. 1999, Kovar-Eder & Wójcicki 2001 and Wójcicki 2001 for references). In gross morphology the fruits of *T. pellendorfensis* are slightly similar to *T. silesiaca* Goeppert reported from Sośnica (Poland, Upper Miocene; Goeppert 1855, Łańcucka-Środoniowa & Zastawniak 1996, Wójcicki & Wilde 2001, Wójcicki & Zastawniak 2002) by having a simple neck without corolla, small tubercles between the upper and lower horns and lower horns located relatively close to the fruit base. However, there are evident differences. For example, *T. silesiaca* is more narrowly obtriangular in outline, truncate at the base, its neck is sunken in the upper surface, and the upper horns are characteristically abruptly raised at the base. The fruits of *T. pellendorfensis* also show some similarities to *T. minuta* Opravil (Opravil 1966; Ostrava-Muglinov, Czech Republic; Pleistocene). These include gross morphology, simple neck without corolla, and presence of small tubercles between upper and lower horns. On the other hand, however, *T. minuta* shares certain characteristics with *T. heerii* Fritsch from the Pliocene of Rippersroda, Germany (Fritsch 1885, Mai et al. 1963). This is especially well visible in the at least slightly elevated upper surface of the fruits and in the raised base of the upper horns.

? Trapaceae

Mikia Kovar-Eder & Wójcicki **gen. nov.**

Type species. *Mikia pellendorfensis* Kovar-Eder & Wójcicki sp. nov.

Diagnosis. Long- and thickly-petiolate, flabellate leaves; leaf margin entire except the adaxial, distal margin, which is more or less regularly dentate, dentate-crenate to slightly serrate; tooth sinus and apex rather rounded, the latter lacking terminal double protrusions (as present in *Trapa*); several veins diverge at the base of the blade, sometimes forking on their way across the lamina.

Derivation of the name. In honour of the eminent Japanese palaeobotanist Shigeru Miki, who contributed essentially to the understanding of the family Trapaceae.

Remarks. In Pellendorf these leaves are associated with nuts of *Trapa pellendorfensis* and *Hemitrapa trapelloidea*. All leaves clearly share the above-described characteristics. None of them have developed double terminal protrusions of the tooth apices, and these leaves therefore do not represent *Trapa* foliage. We suspect that these leaves represent foliage of *Hemitrapa* which is yet unknown, but we lack an explanation for the absence of true *Trapa* leaves in Pellendorf. As evidence for the organic connection of these vegetative and reproductive organs is not available, they are placed in separate genera.

Mikia pellendorfensis Kovar-Eder & Wójcicki **sp. nov.**

Fig. 6: 8–13, Pl. 3, figs 1–8

Holotype. Coll. file No. 2000B0029/14 A.

Paratypes. Coll. file Nos 2000B0008/7 A; 2000B0011/1A–C, 2B; 2000B0029/14 B, C, E, G, I–K, 15 A, B, 16 A, B.

Further material. Coll. file Nos 1999B0056/4–6; 2000B/0008/25, 32; 2000B0011/2 A, C–7, 9–15; 2000B0029/14 D, F, H, L–N, 15 C–F, 16 C, 52–57, 59.

Type locality. Pellendorf, Lower Austria, Austria.

Type horizon. Clays representing marginal facies of Lake Pannon (unit 3 – hydrophyte pelite according Harzhauser et al. in press).

Age. Miocene, Pannonian “zone” C sensu Papp (1951a, 1953).

Derivation of the name. The specific epithet refers to Pellendorf, a village near the *locus classicus* of the species.

Description. Long-petiolate, probably floating leaves, petiole up to at least 125 mm long, width 5–8 mm widening apically and merging into the broad cuneate-decurrent leaf base; lamina flabellate (resembling *Ginkgo*), length of lamina 30–44 mm, width 35–67 mm, ratio length/width 0.5–0.6, margin basally entire, apically distinctly dentate (crenate) to slightly serrate, tooth base and apex rounded, shape of adjacent teeth often slightly varying, so that the margin looks somewhat irregular; venation only faintly traceable, from the apical end of the petiole/leaf base several veins(4–7?) arise, diverging and forking in the lamina (number of forkings remains dubious), the ultimate termination of the veins not recognizable.

Discussion. These leaves were found accumulated in some thin layers of subunit J of the hydrophyte pelite on bedding planes. They are usually covered by a white, Ca-rich layer, as in the case of *Ceratophyllum schrotzburgense*. However, no cell outlines are preserved on the leaves of *Mikia pellendorfensis*. In none of the leaves is the venation well traceable, a phenomenon which is also observable in modern *Trapa* and *Trapella* on the upper leaf surface.

Apart from the lack of the characteristic double terminal protrusions on the tooth apices in *Mikia pellendorfensis, Trapa* foliage differs by having rhombic to deltoid blades. Furthermore, a central main vein is developed in *Trapa* from which second-order veins originate, whereas in *M. pellendorfensis* several almost equally developed veins arise at the transition of petiole/base. The petioles in *Trapa* are long and relatively thick, as in the fossil remains, but swellings like in *Trapa* have not been found in *M. pellendorfensis*.

In *Trapella* (Trapellaceae or Pedaliaceae) the floating leaves are smaller, triangular rounded to subcordate, the petioles are distinctly shorter and slender, and the marginal serration differs by glands developed in the sinuses and by distinct acute/acuminate tooth apices. In *Trapella,* however, several veins originate at the base, diverging and forking in the lamina, and therefore it resembles the here-described fossils.

In gross morphology, *Mikia pellendorfensis* also corresponds to *Centella asiatica* (L.) Urban (Apiaceae), the only aquatic pantropical species of the genus; this makes its placement within Trapaceae uncertain. The foliage of *C. asiatica* resembles *M. pellendorfensis* regarding the long petiole, the general shape of the lamina, the dentation of the distal margin, and especially the venation pattern. Major dif-


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Fig. 7. **1** – *Decodon* sp. (mass-occurrence) and *Carpolithes* gen. et sp. indet., No. 2000B0004/5 scale 1:1; **2**, **3** – *Carpolithes* gen. et sp. indet., scale 2:1, a yet complete infructescense, 2 – No. 2000B0002/7, 3 – No. 2000B0004/24 an already disintegrated infructescence.

ferences of *C. asiatica* concern the slenderness of the petiole, the mostly smaller size of the blades, and their shape, which is usually more reniform to suborbicular than the flabellate blades of *Mikia*. Furthermore, the tooth apices of *C. asiatica* are evidently glanduliferous.

Lythraceae

Decodon sp.

Figs 6: 4–7, 7: 1, Pl. 4, figs 6–11

Material. Due to the mass-occurrence, we restrict our list to only relatively few characteristic specimens.

Coll. file Nos 2000B0002/3, 6, 8A; 2000B0003/5, 7, 10, 11; 2000B0004/3, 4 A–D, 5, 13, 15–17, 20–22, 24, 26, 29; 2000B0006/7, 8 A, B; 2000B0009/35; 2000B0010/1 A, B, 2 A–D, 3–7.

Description. Leaves very variable in size, usually linear, oblong (narrowly oblong, lorate, linear), long leaves sometimes slightly ovate, 60–150(200) mm long, 5–30(–40) mm wide, relation length/width (4–)5–12; leaf base mostly acute, sometimes slightly asymmetric, apex attenuate, leaf margin entire; petiole up to 16 mm long (in specimen coll. file No. 2000B0004/26, which is a small leaf, 20 mm long; Pl. 4, fig. 9), basally wider; midvein very thick, stiff, straight or slightly bent; secondaries thin, densely spaced, usually between 2–4(5) mm; in elliptic, wider specimens up to 6–7 mm, arising under angles of mostly 70–90° (in rarer cases less than that), running almost straight to widely curved towards the leaf margin, in front of which they fuse forming an intramarginal vein; sometimes the secondary veins join in front of the margin, forming loops rather than an intramarginal vein; transitions present; intersecondaries present, sometimes composite intersecondaries; tertiary venation reticulate.

In some specimens (coll. file Nos 2000B0004/4 B, 2000B0010/2) lamina ovate/elliptic, when completed about 80–90 mm long, 43 and 32 mm wide, relation length/width 2.0

←

Fig. 6. If not stated otherwise, all figures natural size. **1** – *Populus mutabilis* Heer, No. 2000B0029/3A; **2** – *Populus balsamoides* Goeppert, No. 2000B0009/2; **3** – *Populus populina* (Brongniart) Knobloch, No. 1999B0051/2; **4–7** – *Decodon* sp.: 4, 6, 7 scale 2:1, 4 – No. 2000B0002/3, 5 – 2000B0006/8 A (on b), 6 – 2000B0002/8 B (on b), 7 – 2000B0010/1; **8–13** – *Mikia pellendorfensis* Kovar-Eder & Wójcicki gen. et sp. nov.: 8 – Paratype No. 2000B0008/7 A, 9 – Paratype, No. 2000B0011/1 B, 10 – No. 2000B0011/4 B, 11 – Paratype, No. 2000B0011/2 B, 12 – Paratype, No. 2000B0011/1 A, 13 – Holotype, No. 2000B0029/14 A

and 2.8; secondary veins brochidodromous, forming loops rather than an intramarginal vein.

Remarks. The short-petioled leaves, their mostly acute leaf base and their smaller length/width ratio match even closer those of the modern *Decodon verticillatus* (L.) Ell. than *D. gibbosus* (E.M. Reid) E.M. Reid, the latter having long petioles, usually cuneate, decurrent leaf bases and higher values of the length/width ratio (Bilina, North Bohemia, Early Miocene, Kvaček & Sakala 1999). However, the only long-petiolate specimen from Pellendorf resembles also *D. gibbosus* from Bilina by its long cuneate/decurrent leaf base (Pl. 4, fig. 9, coll. file No. 2000B0004/26).

These leaves are monodominant in the lower part of the hydrophyte pelite subunits A-G.

Potamogetonaceae

Potamogeton sp.

Pl. 3, fig. 15

Material. Coll. file Nos 2000B0008/51; 2000B0029/13, 21 B, C (imprints, associated with *Ceratophyllum* achene imprints); 2000B0056/7.

Description. Two specimens from washed material, one measuring 2.1 × 1.7 mm, the second 2.0 × 1.6 mm.

Remarks. In addition to these specimens, a few imprints probably also represent this genus.

Smilacaceae

Smilax sagittifera Heer emend. Hantke

Pl. 3, fig. 16

1855 *Smilax sagittifera* Heer; Heer, p. 82, Pl. 30, fig. 7.
1954 *Smilax sagittifera* Heer emend.Hantke; Hantke, p. 82, Pl. 14, fig. 13, Pl. 15, figs 1–2.

Material. Coll. file No. 1997B0019/54.

Description. Leaf shape triangular, base distinctly sagittate, the basal lobes rounded, apex rounded but uppermost part not preserved, length 54 mm (measured from the lowermost margin of the basal lobe to the apex), width 46 mm, margin entire without thorns, only midvein and left hand one of the acrodromously originating lateral veins are well preserved.

Remarks. *Smilax* leaves are usually not abundant, therefore constituting an accessory component in fossil leaf assemblages. The here described leaf derived from the *Taxodium*-rich layer in the gravel pit “Semrad”.

Typhaceae

? ***Sparganium*** sp.

Pl. 3, fig. 14

Material. Coll. file No. 2000B0008/17.

Description. A single imprint of a stalked round infructescence; stalk straight, 6 mm long (incomplete), diameter of infructescence 10 mm; in the center of the imprint deepenings of several fruits distinguishable, at its margin beaks faintly visible.

Remarks. Most probably we are dealing here with a fruiting head of *Sparganium*. Some modern species lack stalked fruiting heads or the stalks are very short only. The relatively long petioles may indicate the basal position of this specimen on a fruiting axis.

Systematic position unknown

Carpolithes gen. et sp. indet.

Fig. 7: 1–3

Material. Coll. file Nos 2000B0002/7; 2000B0003/4; 2000B0004/4, 5, 8=24.

Description. Round imprints of infructescences, about 10–12 mm in diameter, partly devoid of the fruit wall, partly disintegrating, and isolated seed imprints of variable shape, size 1.5–2.0 mm, shape of seed cavity and germination valve sometimes visible.

Remarks. These fructifications and seeds occur associated with *Decodon* leaves, but leaves and fruits have not been found attached to each other. The size of the infructescences is distinctly above that of *D. gibbosus* (Kvaček & Sakala 1999), the modern *D. verticillatus*, and *Microdiptera* (D.H. Mai pers. comm.), but the seed size is close to *Decodon*. From an objective point of view it is quite uncertain whether these infructescences and the *Decodon* leaves belong together; if so, we would be dealing with a new species producing rather big fruits. The poor preservational state, however, hinders a closer determination of these remains.

DISCUSSION

The value of aquatic plants for ecological and climatic interpretation is often underestimated, as has been stated by Mai (1985). In their tectonic, sedimentological, and faunistic context (Harzhauser et al. in press), the here-described assemblages offer new insight in azonal, marginal habitats of "Lake Pannon".

TAPHONOMY

Parautochthonous deposition of the plant remains of the hydrophyte pelite is indicated by the mass-occurrence of usually rarely preserved leaves of *Decodon*, of floating and submerged leaves and shoots of other aquatic plants (*Ceratophyllum*, *Mikia*), as well as by the presence of in situ roots, the co-occurrence of *Ceratophyllum* shoots and fruits, and the presence of still articulate valves of the bivalve *Anodonta*.

ECOLOGY

The hydrophyte pelite of the Pellendorf section documents the existence of coastal freshwater marshland with shallow ponds or lakes at the northwestern margin of "Lake Pannon"; this has never been recorded before. After Harzhauser et al. (in press) in the sedimentary sequence the hydrophyte pelite (unit 3) reflects transitional stages from riverine conditions (underlying gravels of unit 1 and sands of unit 2) to near-coast sands, and finally offshore clays (unit 5).

The monodominance and mass-occurrence of *Decodon* leaves in the lower, partly slightly coarser-grained part of this unit – subunits A to G (Fig. 2, Tab. 3) – clearly documents extended, probably monospecific stands of the water willow as known today from *Decodon verticillatus* in eastern North America.

The slightly finer-grained upper part (subunits I, J; Fig. 2) indicates facial changes and

Table 3. Taxa distribution in the subunits of the hydrophyte pelite. The table includes not only collected material but also field observations. XXX – very abundant, absolutely dominant, XX – abundant, X – present, 1 specimen observed only

	Sand pit "Max" bottom					Sand pit "Max" upper part			Gravel pit "Semrad"
Level	A	B	C	E	G	I	J	upper part-not *in situ*	hydrophyte pelite, probably upper part
Coll. file nos	2000B0006/ 2000B0007/	2000B0005/	2000B0002/ 2000B0003/ 2000B0004/		2000B0010/	2000B0009/	2000B0008/	1999B0056/ 2000B0011/ 2000B0029/	1997B0019/
Nitellopsis majoriformis						XXX	XXX		
Stephanochara aff. *rochettiana*							X		
Taxodium dubium						1			XXX
Nymphaeaceae						XX	XX		
Ceratophyllum schrotzburgense			X			XX	XX		
Ceratophyllum sp.								XX	
Ulmus carpinoides							1		
Populus balsamoides						X			1
Populus mutabilis			1			X		X	
Populus populina	X							1	? 1
Hemitrapa trapelloidea						X	XX		
Mikia pellendorfensis							XX	XX	
Trapa pellendorfensis					X	XX	XX		
Decodon sp.	XXX	XXX	XXX	X	XXX	X	1		
Potamogeton sp.							X	X	
Smilax sagittifera									1
? *Sparganium* sp.							1		
Carpolithes gen. et sp. indet.	X	X	X						

documents quiet, shallow, open waters. Nymphaeaceae, *Potamogeton*, and *Trapa* were rooted dwellers with submerged and floating leaves, while *Ceratophyllum* was free-swimming and almost entirely submerged (Tab. 3). Although we suspect *Mikia pellendorfensis* to constitute the leaves of *Hemitrapa*, the true affinity remains unsolved. Their general appearance, however, with the extremely thick and very long petiole, is reminiscent of aquatic *Trapa*-like plants. Therefore, we tend to interpret these leaves as floating leaves of probably rooted plants. In shallow waters, modern Characeae easily succumb to competition by phanerogams and, if light conditions permit, Characeae inhabit waters up to several meters depth. Similar conditions can be expected at Pellendorf.

Ca-CONTENT

The preservation of the surface of turgescent epidermis cells of *Ceratophyllum schrotzburgense* clearly points towards Ca-precipitation during life time. In waters rich in dissolved Ca (relatively high pH-value), this process is photosynthesis-induced, resulting from CO_2 reduction (Kovar-Eder & Krainer 1990, 1991). The Ca-coated (although not turgescent) leaves of *Mikia pellendorfensis* and the Characeae support this interpretation. However, periodic changes of the ecological parameters are indicated by thin layering in the subunits G, I and J and by the Characeae gyrogonites: the *Nitellopsis majoriformis* gyrogonites from subunit I are well calcified and mature specimens clearly prevail there. Those from subunit J are immature and indicate a deficit during the calcification process.

NUTRIENT CONTENT

Ceratophyllum and *Trapa* may serve as indicators of eutrophic conditions. In Characeae, Nymphaeaceae, *Potamogeton*, and *Sparganium* this is less clear because their modern species include indicators of both eutrophic and oligotrophic conditions. The fossil taxa *Hemitrapa* and *Mikia* do not offer additional information.

INDICATORS OF SALINITY

Regarding the question of a brackish influence in these habitats, no characteristic halophytes are among the recorded taxa, although it cannot be excluded that some species tolerated slightly brackish conditions, e.g. *Potamogeton* (Mai 1985). However, the molluscs documented from the hydrophyte pelite clearly point towards freshwater conditions (Harzhauser et al. in press).

WOODY TAXA

While azonal woody taxa representing possibly riparian or swampy forests are at least poorly documented by *Taxodium dubium* (mass-occurrence), *Populus balsamoides*, *P. mutabilis*, and *P. populina*, representatives of zonal habitats are almost completely absent at Pellendorf. Only *Ulmus carpinoides* may be interpreted as representative of both.

A POSSIBLE MODERN ANALOGUE

The Volga delta in the Astrakhanskiy Biosphere Reserve (northern margin of the Caspian Sea) may serve as a modern analogy in landscape, offering a manifold mosaic of reed and aquatic habitats. Characeae, *Ceratophyllum*, Nymphaeaceae, *Potamogeton*, and *Trapa* are represented there (Baldina et al. 2001). However, the documentation of fossil taxa such as the extinct *Hemitrapa* and *Mikia*, and of *Decodon* – which is presently restricted to eastern regions of North America – distinguishes the fossil deposits of Pellendorf.

BIOSTRATIGRAPHIC REMARKS

Numerous *Trapa*-yielding localities are known in the molasse basin north of the Alps and the eastern Styrian basin (for summary see Kovar-Eder & Wójcicki 2001). They all are dated to the Pannonian (late Miocene). Note, however, that none of the *Hemitrapa* occurrences are conspecific with *Hemitrapa trapelloidea* from Pellendorf: all have been determined as *H. heissigii* from southern Germany – Eberstetten (Gregor 1982), Gallenbach (Schmid & Gregor 1983, Gregor & Schmid 1983), Kirrberg (Riederle & Gregor 1997), Entrischenbrunn (Schmitt & Butzmann 1997), Ursberg (Riederle 1997), Rauscheröd (Gregor 1982, 1986), collection of the Paläontologisches Museum, Munich (unpubl. mat.), and all have been correlated to the late Early Miocene/middle Miocene (Böhme et al. 2002, and

K. Heissig pers. comm.). Moreover, they have never been found associated with *Trapa* fruits. In our opinion, these differences are therefore more likely of biostratigraphic value than facies biased.

CONCLUSIONS

1. The hydrophyte pelite (unit 3; Harzhauser et al. in press) yielded so far unique assemblages of mostly aquatic plants.
2. The taxonomic investigations revealed the first reported unambiguous record of *Hemitrapa trapelloidea* from Europe.
3. For the first time, *Trapa* and *Hemitrapa* co-occur definitively (on the same bedding planes), while all the other rare reports of a co-occurrence were based on misidentifications.
4. *Trapa pellendorfensis* Wójcicki & Kovar-Eder sp. nov. is a new, conspicuous species having only slight similarities to the known *T. silesiaca* and *T. minuta*.
5. *Mikia pellendorfensis* Kovar-Eder & Wójcicki gen. et sp. nov. are probably floating leaves resembling in some features *Trapa*, *Trapella*, and *Centella* foliage but also differing from them essentially. It is not excluded that these leaves represent the foliage of *Hemitrapa trapelloidea* fruits.
6. Thus, Pellendorf offers new insight in the marginal habitats at the northwestern margin of “Lake Pannon”. Coastal freshwater marshland with ponds and lakes may be reconstructed based on the plant remains. This is consistent with the sedimentological and faunistic results (Harzhauser et al. in press).
7. Extensive, probably monodominant stands of *Decodon* are documented in the lower part of the hydrophyte pelite (subunits A to G).
8. The upper part (subunits I-J) bears species-richer aquatic assemblages, indicating a facies shift towards shallow open water with *Ceratophyllum*, Characeae, *Hemitrapa*, *Mikia* gen. nov., Nymphaeaceae, *Potamogeton*, and *Trapa*. *Sparganium* represents a reed element.
9. Azonal woody elements pointing towards riparian or swampy forest habitats are rare (*Populus balsamoides, P. mutabilis, P. populina* and *Taxodium dubium* – in one local mass-occurrence only), while zonal ones are almost absent. Only *Ulmus carpinoides* may be assigned to both.

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PLATES

Plate 1

1–10. *Trapa pellendorfensis* Wójcicki & Kovar-Eder, sp. nov., **h** – harpoon, **lh** – lower horn**,** **n** – neck, **nb** – neck base, **t** – tubercle, **uh** – upper horn. **1** – Holotype, No. 2000B0009/3; **2–10** – Paratypes. 2 – No. 2000B0029/34 A, 3 – No. 2000B0029/34 C, 4 – No. 2000B0008/23 C, 5 – No. 2000B0008/23 B, 6 – No. 2000B0008/23 A, 7 – No. 2000B0029/35, 8 – No. 2000B0029/36, 9 – No. 2000B0029/33, 10 – No. 2000B0029/34 B

11–13. *Nitellopsis majoriformis* (Papp) Schwarz comb. nov., mature specimens, 11 – apical view, 12 – lateral view, 13 – basal view; 11, 12 – No. 2000B0009/38/2, 13 – No. 2000B0009/38/4

14–16. *Nitellopsis majoriformis* (Papp) Schwarz comb. nov., immature specimens, 14 – apical view, 15 – lateral view, 16 – basal view, 14 – No. 2000B0008/53/1, 15, 16 – No. 2000B0008/53/2

17–19. *Stephanochara* aff. *rochettiana* (Heer) Feist-Castel, 17 – apical view, 18 – lateral view, 19 – basal view, 11 – No. 2000B0008/52/1, 12, 13 – No. 2000B0008/52/2

20. *Nitellopsis meriani* (Braun ex Unger) Grambast & Soulié-Märsche, lateral view, Mainz Basin, Chattian

21. *Nitellopsis majoriformis* (Papp) Schwarz comb. nov., mature specimen; lateral view. No. 2000B0009/38/5

Scale bars 1 cm


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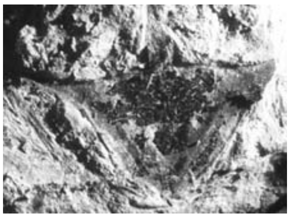
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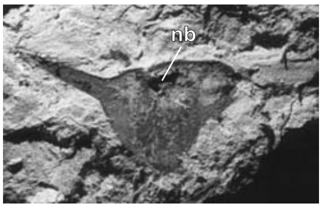

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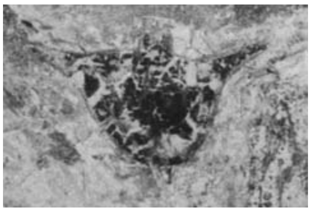
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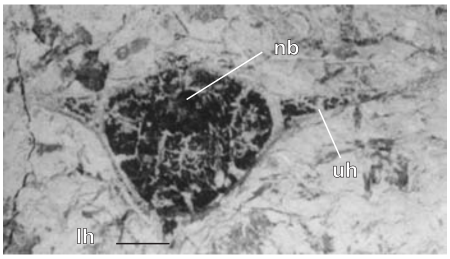

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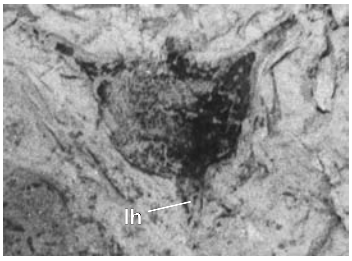

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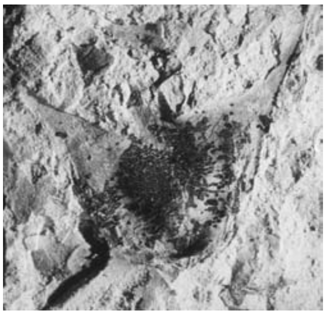
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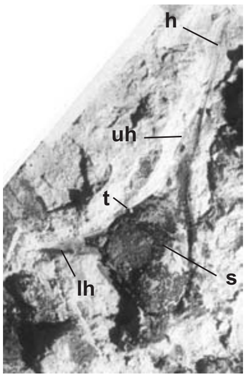

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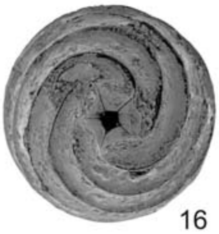
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Plate 2

1–12. *Hemitrapa trapelloidea* Miki, imprints from Pellendorf: 1 – No. 2000B0008/1, 2 – No. 2000B0009/15, 3 – No. 2000B0029/19, 4 – No. 2000B0029/20, 5 – No. 2000B0029/21, 6 – No. 2000B0029/22, 7 – No. 2000B0029/23, 8 – No. 2000B0029/24, 9 – No. 2000B0008/22, 10 – No. 2000B0029/25, 11 – No. 2000B0029/26, 12 – No. 2000B0029/27

13–15. *Hemitrapa trapelloidea* Miki, specimens (topotypes) from the Seto Porcelain Clay Formation of Akazu mine, Seto City, Aichi Prefecture, Central Honshu, Japan, coll. K. Uemura 1980 (Natural Science Museum, Tokyo, Japan); 13 – compressed fruit and fragment of arm with harpoon, 14 – reverse of 15

Scale bars 1 cm


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Plate 3

1–8. *Mikia pellendorfensis* Kovar-Eder & Wójcicki gen. et sp. nov.; 1 – paratype, No. 2000B0029/16, 2 – holotype, No. 2000B0029/14 A, 3 – paratype, No. 2000B0029/15 B, 4 – paratype, No. 2000B0029/15 A, 5 – paratype, 2000B0008/7 A, 6–8 scale 2:1, distal leaf margin, dentation, 6 – holotype, No. 2000B0029/14 A, 7 – paratype, No. 2000B0029/14 B, 8 – paratype, No. 2000B0008/7

9. *Ulmus carpinoides* Goeppert emend. Menzel, No. 2000B0008/29

10. *Taxodium dubium* (Sternberg) Heer, No. 1997B0019/1

11–13. *Ceratophyllum* sp., scale 3:1, 11 – No. 2000B0029/7, 12 – No. 2000B0029/12 A, 13 – No. 2000B0029/6 A

14. ?*Sparganium* sp., scale 2:1, No. 2000B0009/17 (on b)

15. *Potamogeton* sp., scale 15:1, No. 2000B0056/7

16. *Smilax sagittifera* Heer emend. Hantke, No. 1997/0019/54

Unless otherwise stated × 1


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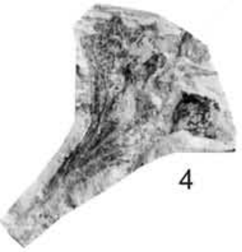
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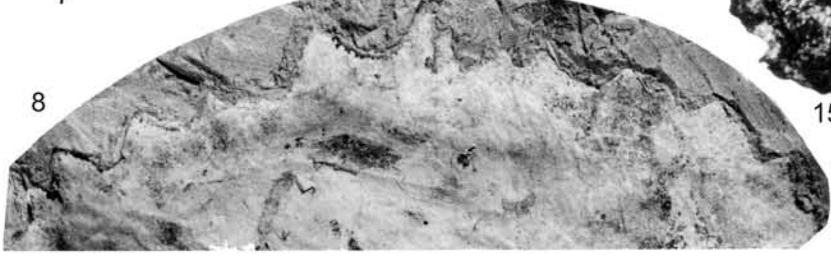
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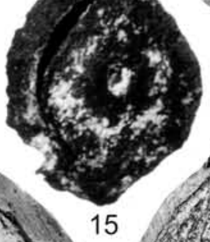
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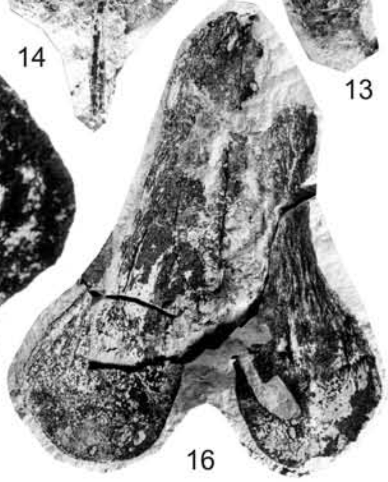

16

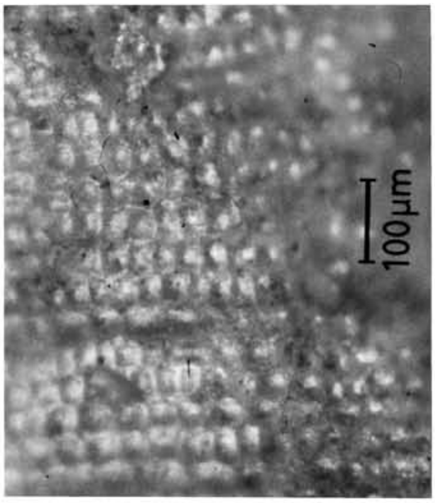
Plate 4

1–4. *Ceratophyllum schrotzburgense* Hantke, 1 – No. 2000B0008/43, scale 1.5:1, 2 – No. 20000B0008/50, 3 – No. 2000B0008/14, 4 – No. 2000B0008/50

5a,b. Nymphaeaceae, No. 2000B0008/19, b scale 3:1

6–11. *Decodon* sp., 6 – No. 2000B0002/3, 7a,b – No. 2000B0010/1 A, b scale 2:1, 8a,b – No. 2000B0002/8 B, b scale 3:1, 9 – No. 2000B0004/26, 10 – No. 2000B0010/2 B, 11a,b – No. 2000B0002/8 A, a scale 2:1

Unless otherwise stated × 1



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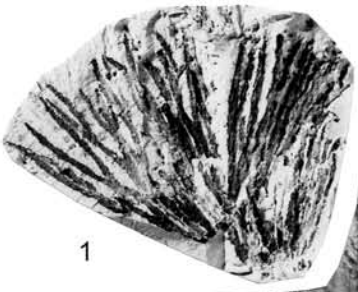
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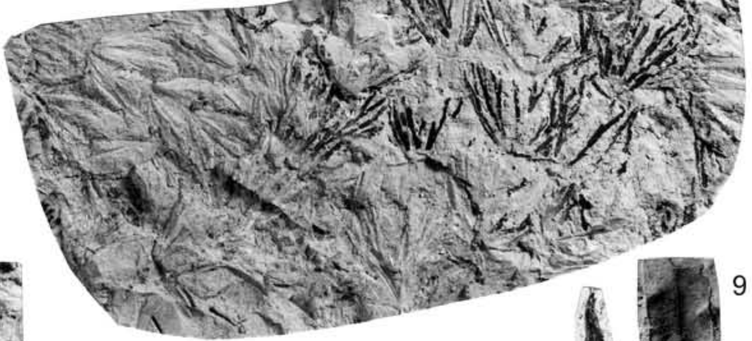

2


5a


4


6


8a


9

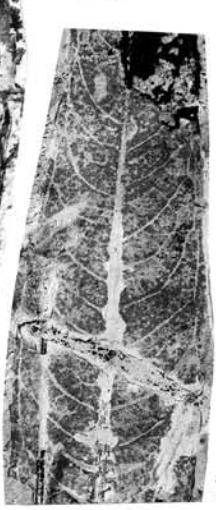

7a


5b


10


11a


11b


7b


8b