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Trapaceae from the late Miocene of Austria and the European context*

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ABSTRACT. Fossil fruits of *Trapa* L. and *Hemitrapa* Miki (Trapaceae) known from eight late Miocene Austrian localities are characterized. Fruits morphologically intermediate between *Trapa ungeri* Wójcicki & Kovar-Eder and *T. srodoniana* Wójcicki from Hinterschlagen (Upper Austria, Pannonian) are described as a new species *T. spectabilis* Wójcicki & Kovar-Eder sp. nov. Additional morphological characteristics of *T. srodoniana* are provided and the species description is emended. The description of *T. silesiaca* Göpp. emend. Wójcicki & Zastawniak is supplemented and numerous specimens from Austria are figured. Fossil fruits and pollen of definite Trapaceae (*Trapa* L., *Hemitrapa* Miki) and leaves of probable Trapaceae affinity (*Mikia* Kovar-Eder & Wójcicki) from Austria are brought into an European aspect. The stratigraphical relevance of members of the Trapaceae is brie y discussed and the ecology based on fossil assemblages is brie y characterized. The pollen spectrum from Pellendorf (Lower Austria, Pannonian) is provided which includes mesophytic taxa.

KEY WORDS: Trapaceae, *Trapa*, *Hemitrapa, Mikia,* fossil fruit, leaf, pollen, morphology, new species, ecology, putative hybridization, Neogene, Miocene, Austria, Europe

INTRODUCTION

During the last decade an enormous amount of new data about fossil *Trapa* L. and *Hemitrapa* Miki from Europe became available. However, the records remained spotty and, so far, were never synthesized. In this paper, we provide detailed characteristics of fruits intermediate between *Trapa ungeri* Wójcicki & Kovar-Eder and *T. srodoniana* Wójcicki from Hinterschlagen (Upper Austria, Pannonian) brie y described by Kovar-Eder and Wójcicki (2001), and an emended description of *T. srodoniana* and *T. silesiaca* Göppert emend. Wójcicki & Zastawniak. Descriptions of another two species of the Trapaceae from the Pannonian of Austria, *Hemitrapa trapelloidea* Miki and *Trapa pellendorfensis* Wójcicki & Kovar-Eder, and of *Mikia pellendorfensis* Kovar-Eder & Wójcicki that may represent foliage of *Hemitrapa* have been published earlier (Kovar-Eder & Wójcicki 2001, Kovar-Eder et al. 2002). The rich evidence of the Trapaceae from Austria (Fig. 1, Tab. 1) is synthesized then and brought into an European aspect. We also discuss the ecology based on fossil assemblages and the stratigraphical relevance of members of the Trapaceae which was neglected so far. In this context, we refer to the stratigraphic schemes for the Lower/Middle Miocene by Ćorić et al. (2004) and Upper Miocene by Harzhauser et al. (2004).

The material from Austria is housed in the collections of the Geological-Palaeontological Department of the Natural History Museum Vienna (NHMW), the Institute of Palaeontology

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Table 1. Fossil records of the Trapaceae from Austria

Taxon	Revision and references		Locality	Basin	Age	Reference
Trapa heeri Fritsch	*Trapa silesiaca* Göpp.	Kovar-Eder & Krainer 1990 and this paper	Rohrbach near Ziersdorf, Lower Austria	N part of the Vienna basin	Miocene, early Pannonian	Kovar 1979
Hemitrapa trapelloidea Miki			Pellendorf, Lower Austria	N part of the Vienna basin	Miocene, Pannonian "zone" C	Kovar-Eder et al. 2002
Trapa pellendorfensis Wójcicki & Kovar-Eder			Pellendorf, Lower Austria	N part of the Vienna basin	Miocene, Pannonian "zone" C	Kovar-Eder et al. 2002
Mikia pellendorfensis Kovar-Eder & Wójcicki			Pellendorf, Lower Austria	N part of the Vienna basin	Miocene, Pannonian "zone" C	Kovar-Eder et al. 2002
Sporotrapoidites illingensis Klaus (Trapa)			Badersdorf, Burgenland	Pannonian basin	Miocene, Pannonian "zone" F	Zetter & Ferguson 2001
Trapa heeri Fritsch	*Trapa silesiaca* Göpp.	Kovar-Eder & Krainer 1990 and this paper	Höllgraben, Styria	Eastern Styrian basin	Miocene, Pannonian "zone" A, B	Kovar-Eder & Krainer 1988
Trapa silesiaca Göpp.			Wörth, Styria	Eastern Styrian basin	Miocene, Pannonian "zone" C	Kovar-Eder & Krainer 1990
Trapa silesiaca Göpp.			Mataschen, Styria	Eastern Styrian basin	Miocene, Pannonian "zone" B	Meller & Hofmann 2004
Trapa (pollen)			Mataschen, Styria	Eastern Styrian basin	Miocene, Pannonian "zone" P	Meller & Hofmann 2004
Trapa srodoniana Wójcicki			Hinterschlagen, Upper Austria	Molasse basin	Miocene, Pannonian	Kovar-Eder & Wójcicki 2001
Trapa ungeri Wójcicki & Kovar-Eder			Hinterschlagen, Upper Austria	Molasse basin	Miocene, Pannonian	Kovar-Eder & Wójcicki 2001
Trapa spectabilis Wójcicki & Kovar-Eder, sp. nov.	*Trapa ungeri*/*T. srodoniana* putative hybrids	this paper	Hinterschlagen, Upper Austria	Molasse basin	Miocene, Pannonian	Kovar-Eder & Wójcicki 2001
Sporotrapoidites illingensis Klaus (*Trapa*)			Hinterschlagen, Upper Austria	Molasse basin	Miocene, Pannonian	Zetter & Ferguson 2001
Trapa heeri Fritsch	*Trapa silesiaca* Göpp.	Kovar-Eder & Krainer 1990 and this paper	Großenreith, Upper Austria	Molasse basin	Miocene, Pannonian	Kovar-Eder 1988
Trapa (pollen)			Großenreith, Upper Austria	Molasse basin	Miocene, Pannonian	Zetter in Kovar-Eder 1988
Trapa heeri Fritsch	*Trapa silesiaca* Göpp.	Kovar-Eder & Krainer 1990 and this paper	Lohnsburg, Upper Austria	Molasse basin	Miocene, Pannonian	Kovar-Eder 1988
Trapa (pollen)			Lukasberg, Upper Austria	Molasse basin	Miocene, ? late Sarmatian/Pannonian	Masselter & Hofmann 2005

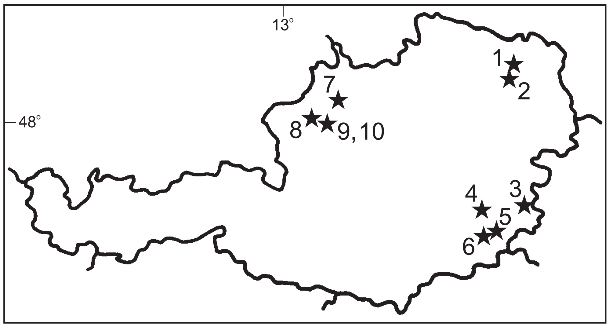


Fig. 1. Sketch map of Austria showing the occurrences of fossil *Trapa* (1–10), *Hemitrapa* (2), and *Mikia* (2). **1** – Rohrbach near Ziersdorf, **2** – Pellendorf, **3** – Badersdorf, **4** – Höllgraben, **5** – Wörth, **6** – Mataschen, **7** – Hinterschlagen, **8** – Großenreith near Lohnsburg, **9** – Lohnsburg, **10** – Lukasberg

of the University of Vienna (IPUW) and the Bayerische Staatssammlung für Paläontologie und Geologie in Munich (BSP).

SYSTEMATIC PART

Trapa silesiaca Göppert emend. Wójcicki & Zastawniak

Fig. 2: 1–40

1852 *Trapa silesiaca* Göpp. nom. nud.; Göppert, p. 495.
1852 *Trapa bifrons* Göpp. nom. nud.; Göppert, p. 495.
1855 *Trapa silesiaca* Göpp.; Göppert, p. 38, Pl. 25, fig. 14.
1855 *Trapa bifrons* Göpp.; Göppert, p. 38, Pl. 25, fig. 15.
1919 *Trapa silesiaca* Göpp.; Meyer, p. 174, Pl. 15, fig. 6 & 7.
1920 *Trapa silesiaca* Göpp.; Kräusel, p. 384, Pl. 23, fig. 27 & 31.
1973 *Trapa kräuselii* V.N. Vassil. sp. nov.; Vassilev, p. 210, Fig. 1: 12.
1979 *Trapa heeri* Fritsch; Kovar, p.110, Abb. 3, Pl. 1, figs 1–6.
1987 *Trapa heeri* Fritsch; Kovar, p. 208.
1988 *Trapa heeri* Fritsch; Kovar-Eder, p. 47, Pl. 5, figs 10–14.
1988 *Trapa heeri* Fritsch; Kovar-Eder & Krainer, p. 36, Pl. 1, fig. 4.
1990 *Trapa silesiaca* Göpp.; Kovar-Eder & Krainer, p. 20, Pl. 1, figs 14, 15.
1996 *Trapa silesiaca* Göpp.; Zastawniak et al., p. 901, Pl. 299, fig. 13.
?1998 *Trapa silesiaca* Göpp.; Krajewska, p. 51, Fig. 12: 11–19, Pl. 6, figs 3–10.
2001 *Trapa silesiaca* Göpp.; Wójcicki & Wilde, p. 20, Fig. 3a, b.
2002 *Trapa silesiaca* Göpp. emend. Wójcicki & Zastawniak; Wójcicki & Zastawniak, p. 30, Figs 1, 2.
2004 *Trapa silesiaca* Göpp.; Meller & Hofmann, p. 214, Pl. 2, figs 7, 8.

M a t e r i a l. Rohrbach near Ziersdorf – Coll. file Nos NHMW 1978/2003, Ia/2 (Kovar 1979, Fig. 3; Pl. 1, fig. 5a,b), III/7 (Kovar 1979, Pl. 1, fig. 2a,b), IV/13 (Kovar 1979, Pl. 1, fig. 1a,b), XIXa/28 (Kovar 1979, Pl. 1, fig. 3a,b), XXI/30 (Kovar 1979, Pl. 1, fig. 6a), XXVIa/24 (Kovar 1979, Pl. 1, fig. 4); Figures in this paper (Fig. 2: 15, 16, 17, 18, 19) – coll. file No. 1978/2003.

Höllgraben near Weiz – Coll. file Nos NHMW 1984/72/25 (Kovar-Eder & Krainer 1988, Pl. 1, fig. 4), 1984/72/26 (Fig. 2: 5).

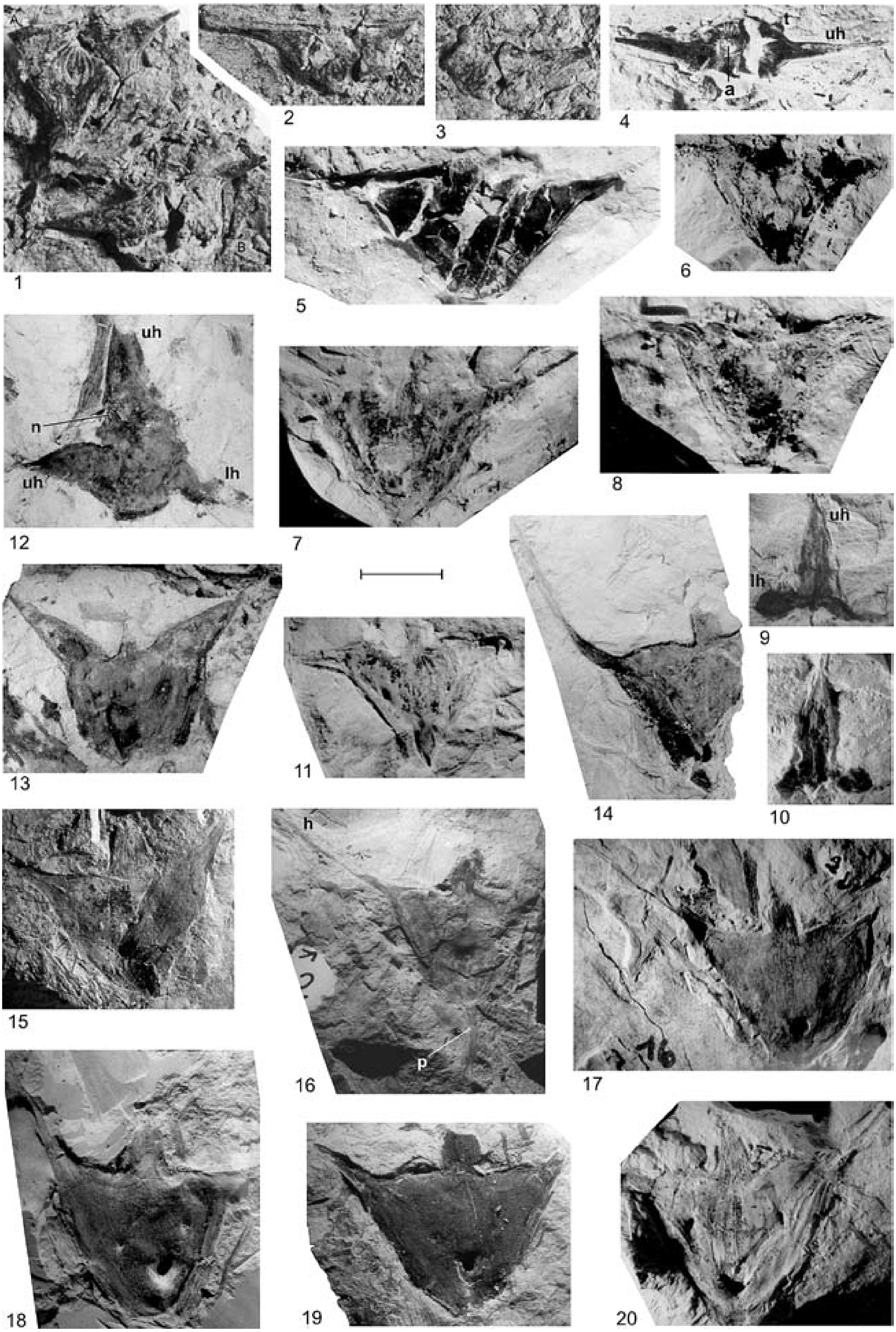
Wörth – Coll. file Nos NHMW 1987/44/230, 238, 241, 245 (Kovar-Eder & Krainer 1990; Pl. 1: 14), 1987/44/245a (Fig. 2: 14, counterpart), 1987/44/246, 248 (Fig. 2: 12), 1987/44/258 (Kovar-Eder & Krainer 1990; Pl. 1: 15), 1987/44/266 (Fig. 2: 13, counterpart of 258).

Großenreith near Lohnsburg – Coll. file Nos NHMW 1980/15/39 (Fig. 2: 5), 1980/15/40, 41, 42, 43, 44, 45, 48, 49, 53 (Kovar-Eder 1988, Pl. 5, fig. 12).

Lohnsburg – Coll. file Nos NHMW 1982/84, 1982/84/66/1, 4a (Kovar-Eder 1988, Pl. 5, fig. 11), 1982/84/66/5, 6, 7, 8a,b, 9 (Fig. 2: 34), 1982/84/67, 89; 1985/68/31, 32, 33, 34, 35 (Fig. 2: 22), 1985/68/36 (Fig. 2: 40), 1985/68/38 (Fig. 2: 20), 1985/68/43 (Fig. 2: 36), 1985/68/45 (Fig. 2: 29), 1985/68/46 (Fig. 2: 21), 1985/68/47 (Fig. 2: 30; counterpart of 1985/68/45), 1985/68/48 (Fig. 2: 35), 1985/68/51, 52, 53 (Kovar-Eder 1988, Pl. 5, fig. 12), 1985/68/55, 56 (counterpart of 1985/68/59), 1985/68/57 (counterpart of 1985/68/53), 1985/68/59 (Fig. 2: 28), 1985/68/60 (Fig. 2: 24), 1985/68/61, 62 (Fig. 2: 26), 1985/68/63, 64, 65 (Kovar-Eder 1988, Pl. 5, fig. 13), 1985/68/66, 67 (Fig. 2: 38), 1985/68/68, 70 (Fig. 2: 23), 1985/68/84; collective No. BSP 1978, coll. E. Rieber, ca. 70 specimens (Fig. 2: 25, 27, 31, 32, 33, 37, 39).

Mataschen – Coll. file Nos NHMW 1998B0014/1A,B, 2, 3, 4; Coll. file No. IPUW 2003-2-7, 8 (Meller & Hofmann 2004, Pl. 2, figs 7, 8).

E m e n d e d d e s c r i p t i o n. Fruits of small or medium size, regularly obtriangular in outline, with two pairs of horns; fruit 9–26 mm high (including neck), width of fruit at upper horns 14–38 mm; fruit about 1.3–2.2 times as wide as high; fruit head pronounced, (3–)5–12 mm long, its upper end located below the line joining the raised bases of the upper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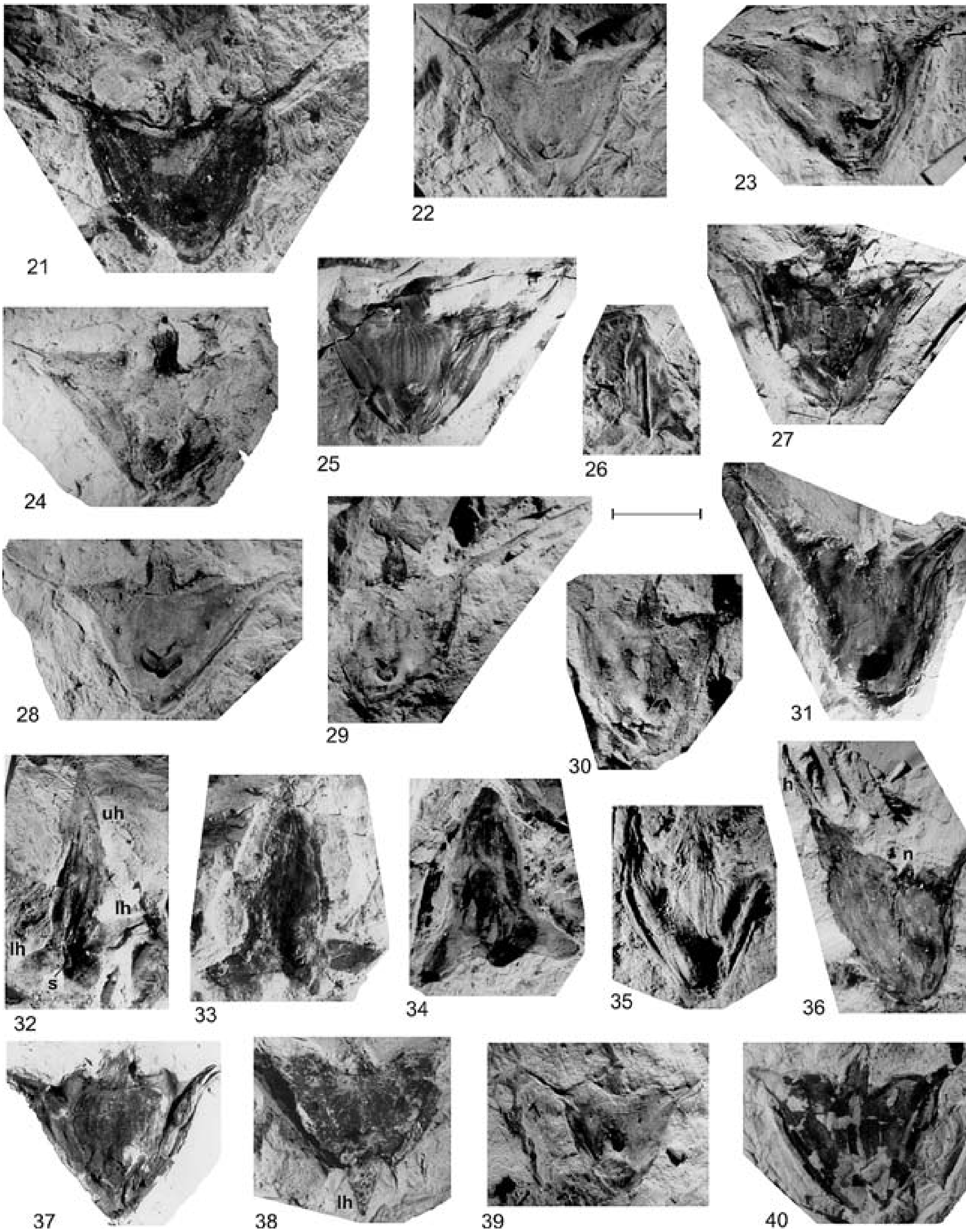


Fig. 2. *Trapa silesiaca* Göpp. emend. Wójcicki & Zastawniak from: **1–4** – Mataschen, **5** – Höllgraben, **6–11** – Großenreith, **12–14** – Wörth, **15–19** – Rohrbach, and **20–40** – Lohnsburg. (**1** – No. NHMW 1998B0014/1A, B, **2** – No. NHMW 1998B0014/2, **3** – No. NHMW 1998B0014/3, **4** – No. NHMW 1998B0014/4 **5** – No. NHMW 1984/72/26, **6** – No. NHMW 1980/15/42, **7** – No. NHMW 1980/15/49, **8** – No. NHMW 1980/15/39, **9, 10** – No. NHMW 1980/15/87a,b (part and counterpart), **11** – No. NHMW 1980/15/45, **12** – No. NHMW 1987/44/0248, **13** – No. NHMW 1987/44/0266, **14** – No. NHMW 1987/44/0245a, **15 –19** – No. NHMW 1978/2003, **20** – No. NHMW 1985/68/38, **21** – No. NHMW 1985/68/46, **22** – No. NHMW 1985/68/35, **23** – No. NHMW 1985/68/70, **24** – No. NHMW 1985/68/60, **26** – No. NHMW 1985/68/62, **28** – No. NHMW 1985/68/59, **29** – No. NHMW 1985/68/45, **30** – No. NHMW 1985/68/47 (counterpart of 1985/68/45), **34** – No. NHMW 1985/68/9, **35** – No. NHMW 1985/68/48, **36** – No. NHMW 1985/68/43, **38** – 985/68/67, **40** – 1985/68/36; **25**, **27**, **31–33**, **37**, **39** – BSP collective No. 1978, coll. E. Rieber). **a** – apical aperture, **h** – harpoon, **n** – neck, **lh** – lower horn, **uh** – upper horn, **p** – impression of pedicel, **s** – scar, **t** – tubercle; scale bars 1 cm

horns, bearing a well developed neck sometimes slightly broadening towards the base; neck 1.5–3.5(–5.5) mm long and 2.0–4.5(–5.5) mm broad, usually at least slightly protruding beyond the line joining the bases of the upper horns, corona lacking; apical aperture with a ring of upward-pointing hairs; surface of fruit head and neck finely ribbed; upper horns narrowly triangular in outline, 6–15(–19) mm long, characteristically raised at the base, gradually attenuate into straight elongate, thin, spine-like tips, ascending (25º–75º), with a smooth surface except for the at least 6–11 mm long, retrorsely barbed spines (harpoons); presence of mat areas excluded; lower horns at least slightly retrorse, straight, up to 8 mm long, inserted usually slightly asymmetrically in 1/5 to 2/5 from the fruit base or slightly below, sometimes with small cavity at the base on the abaxial side; frame of the fruit well developed; on the fruit frame between the bases of the upper and lower horns, small, conical tubercles up to 1 mm long developed; lower part of the fruit body regularly obtriangular in outline, slightly truncate at the base, its surface (on one side only) covered with five protruding longitudinal ribs; fruit base with a small smooth ring, up to 1.5 mm high; basal scar small, up to 1.5 mm in diameter.

Remarks. Revision of the material indicated that *T. silesiaca* occurred at six Pannonian localities in Austria (Fig. 1, Tab. 1). After careful examination of the two *T. silesiaca* specimens from Sośnica (Schossnitz) housed in the Natural History Museum, Berlin, figured by Kräusel (1920) and discovery of traces of lower horns, the Austrian material from Rohrbach (Kovar 1979), Großenreith (Kovar 1987), Höllgraben (Kovar-Eder & Krainer 1988) and Lohnsburg (Kovar-Eder 1988) originally identified as *T. heeri* have been reclassified and included into *T. silesiaca* by Kovar-Eder (in Kovar-Eder & Krainer 1990). Later reinvestigation of Göppert's type material and new material collected at the locus classicus resulted in formal lectotypification of *T. silesiaca* and emendation of diagnosis (Wójcicki & Zastawniak 2002). Abundant material from Austria and different positions of fruits in the sediment enabled a more precise characterization of the species variability and the emendation of its description. Fruits preserved as compressions/impressions along the plane of

Table 2. Comparison of extreme values of nine parameters of *Trapa silesiaca* from six localities in Austria and from the species locus classicus (Sośnica, Poland) including type specimens. Number of specimens in [ ]

Character / Locality	Großenreith	Höllgraben	Lohnsburg	Mataschen	Rohrbach	Wörth	Sośnica
Height of fruit (mm)	14–18 [5]	17–18 [2]	11–21 [28]	13 [1]	18–26 [10]	15–20 [3]	9–14 [16]
Width of fruit (mm)	30–33 [4]	28–38 [2]	18–34 [25]	19 [1]	26–35 [11]	28–37 [3]	14–26 [17]
Length of upper horn (mm)	10–12 [5]	9–14 [2]	7–14 [28]	9–11 [4]	9–19 [9]	12–15 [3]	6–11 [19]
Length of lower horn (mm)	6 [1]	6 [1]	5–8 [10]	4–6 [2]	7 [1]	8 [1]	4–5 [3]
Length of neck (mm)	2.0–3.0 [5]	3.0–3.5 [2]	1.5–3.0 [31]	1.5–2.0 [2]	3.0–5.5 [10]	2.0–3.0 [3]	1.5–3.0 [20]
Angle of upper horn (°)	60–75 [5]	20–25 [2]	45–70 [23]	55 [1]	30–60 [10]	25–40 [3]	35–55 [19]
Width/height of fruit	1.76–2.14 [4]	1.56–2.23 [2]	1.25–2.08 [20]	1.46 [1]	1.28–1.77 [10]	1.60–1.87 [3]	1.27–2.00 [14]
Distance of lower horn from fruit base /fruit height	0.24–0.33 [4]	0.24–0.28 [2]	0.20–0.36 [25]	0.35 [1]	0.19–0.31 [10]	0.20–0.33 [3]	0.22–0.31 [15]
Lenght of neck/height of fruit	0.12–0.18 [4]	0.18–0.19 [2]	0.11–0.22 [25]	0.12 [1]	0.16–0.24 [10]	0.13–0.15 [3]	0.12–0.21 [14]

the lower horns definitely clarify the problem concerning the presence of well-developed, solid lower horns in *T. silesiaca* fruits (Fig. 2: 9, 10, 26, 32–34).

Trapa silesiaca is a more variable species than previously supposed (cf. Wójcicki & Zastawniak 2002). However, no consistent morphological differences were noted within the fossil record between the Austrian localities (Fig. 2; see also additional specimens figured in Kovar 1979, 1987, Kovar-Eder 1988, Kovar-Eder & Krainer 1988, 1990, Meller & Hofmann 2004). There are some differences in fruit size between localities but the ranges overlap considerably (Tab. 2). Bigger fruits tend to occur in the population at Rohrbach but at localities where numerous specimens are available (Lohnsburg) it becomes clear that there is a continuous range of size and shape of fruits (Fig. 2, Tab. 2). Additionally, it should be noted that the variability of fruit size is enlarged further by different preservation of specimens at different localities (oxidized, mummified or coalified endocarps, or their impressions). The inclination of upper horns is a most variable character and mainly depending on the deformation and/or position of the fruit in the sediment. Generally, the variability of *T. silesiaca* fruits is comparable to that observed in modern *Trapa* species (e.g. Staszkiewicz & Wójcicki 1979, 1981, Kadono 1987, Tzvelev 1993).

From the preliminary investigations of numerous fossil *Trapa* specimens from Europe it seems that *T. silesiaca* was probably the most common representative of the genus in the European late Miocene, but, does not continue into the Pliocene (cf. Wójcicki & Zastawniak 2002, 2003), however, this problem requires more material and further detailed studies.

Trapa srodoniana Wójcicki

Fig. 3: 10–18

1990 *Trapa silesiaca* Göppert; Stuchlik et al., Pl. 14.

1998 *Trapa srodoniana* Wójcicki sp. nov.; Wójcicki & Zastawniak, p. 170, Fig. 3a–i.

2001 *Trapa srodoniana* Wójcicki; Kovar-Eder & Wójcicki, p. 234, Pl. 6, fig. 6.

Material. Tagebau Heissler near Hinterschlagen, Hausruck lignite area. Coll. file Nos NHMW 1988/0138/1 (Fig. 3: 10), 1988/0138/7 (Fig. 3: 17), 1988/0138/8 (Fig. 3: 12), 1988/0138/22; 2000B0014/5 (Fig. 3: 13); 2001B0010/2 (Fig. 3: 16), 2001B0010/3 (Fig. 3: 11), 2001B0010/4 (Fig. 3: 18), 2001B0010/5 (Fig. 3: 15), 2001B0011 (Fig. 3: 14).

Emended description. Fruits of medium size, with two massive extended horns, broadly obtriangular in outline; fruit (5–)12–16 mm high (including neck), width of fruit at upper horns (16–)19–33 mm, fruit about (0.3?)0.5–0.8 as high as wide; head of the fruit pronounced, its upper end located somewhat below the line joining the raised bases of the upper horns; neck well developed, 1–4 mm high; apical aperture up to 3 mm in diameter, rounded, a ring of upward pointing hairs closing the apical aperture usually visible; surface of the fruit head and neck finely ribbed; corona lacking; upper horns (4.5–)6–13 mm long, patent to slightly upward pointing, narrowly triangular in outline, bearing damaged or sometimes ± complete thin spines up to ca. 5 mm long, with retrorse barbs (harpoons), horns visibly raised at the base; the presence of mat areas excluded; lower horns reduced to rounded tuberculate structures, 0.5–2.5 mm long, located usually in the centre of the fruit body or somewhat above, sometime with small well-developed conical tubercle at the base on the abaxial side; frame of the fruit well developed with solid, usually truncate tubercles, up to 2.5 mm long, inserted between the upper and lower horns; lower part of the body of the fruit broadly obtriangular in outline, its surface covered with five protruding longitudinal ribs (visible on one side of the fruit); base of fruit characteristically abruptly narrowed, sometimes rounded, stalked or with a very small scar with irregular margin; length of its narrow part (including stalk when present) up to 4 mm.

Remarks. *Trapa srodoniana*, a fossil species of unique morphology originally described from Bełchatów, Middle Poland (Wójcicki & Zastawniak 1998), has been identified in the Pannonian material from Hinterschlagen in Upper Austria (Kovar-Eder & Wójcicki 2001). Recent stratigraphical investigations of sediments in Bełchatów indicated that the *T. srodoniana* bearing horizon "Bełchatów VIb" is late Miocene (Pannonian) in age (Szynkiewicz 2000), but not late Miocene–early Pliocene (Stuchlik et al. 1990) or Pliocene (Wójcicki & Zastawniak 1998).

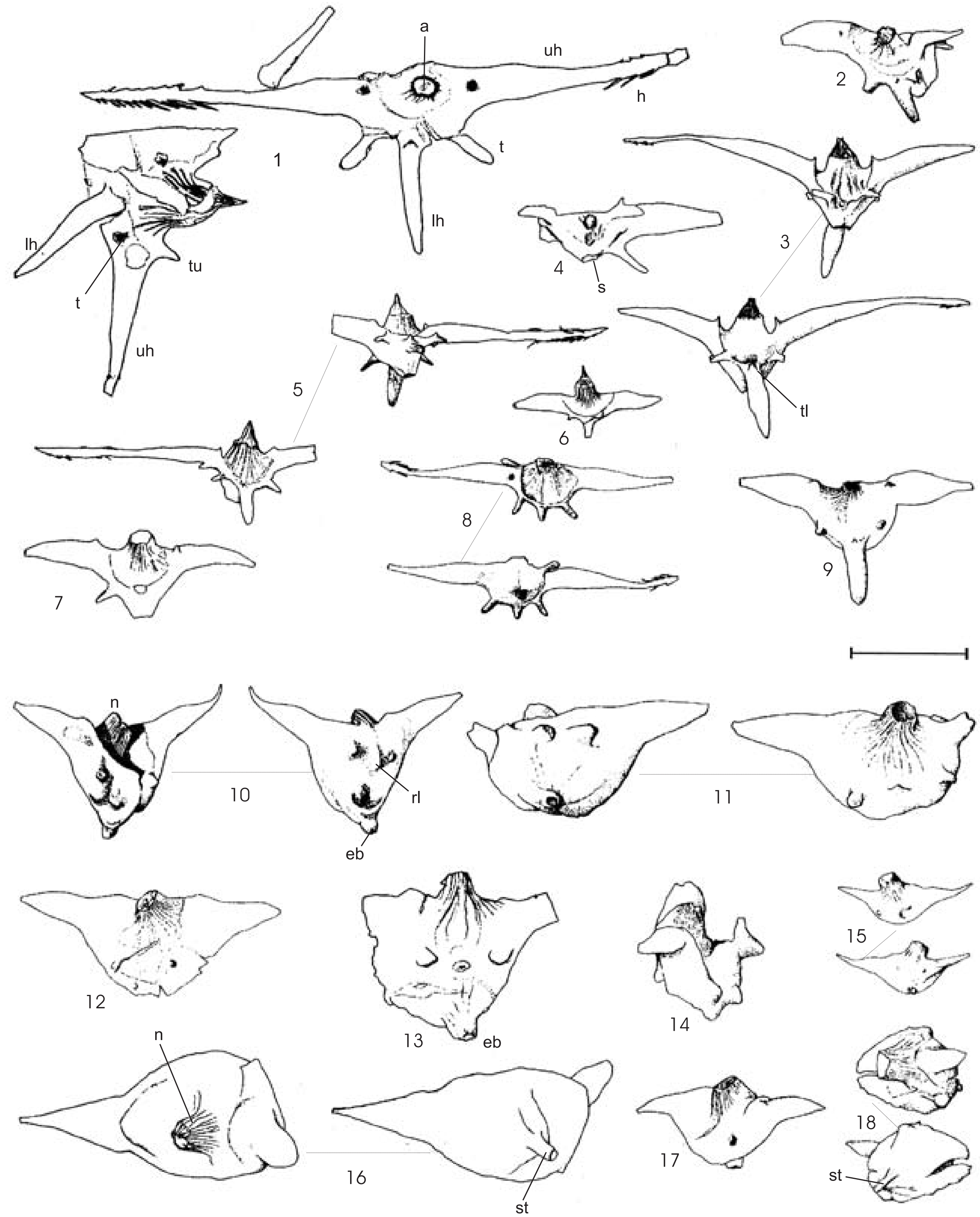


Fig. 3. **1–9** *Trapa ungeri* Wójcicki & Kovar-Eder (**1** – No. NHMW 1988/0138/3 A,B, **2** – No. NHMW 2000B0014/3, **3** – No. NHMW 2000B0014/2, **4** – No. NHMW 2000B0014/4, **5** – No. NHMW 2000B0014/1, **6** – No. NHMW 2001B0010/1, **7** – No. NHMW 1988/0138/6, **8** – No. NHMW 2000B0014/6, **9** – No. NHMW 1988/0138/19 (2–4, 6 **–** paratypes, 5 – holotype), and **10–18** *T. srodoniana* Wójcicki (**10** – No. NHMW 1988/0138/1, **11** – No. NHMW 2001B0010/3, **12** – No. NHMW 1988/0138/8, **13** – No. NHMW 2000B0014/5, **14** – No. NHMW 2001B0011, **15** – No. NHMW 2001B0010/5, **16** – No. NHMW 2001B0010/2, **17** – No. NHMW 1988/0138/7, **18** – No. NHMW 2001B0010/4) from Tagebau Heissler near Hinterschlagen. Figs 1–5 and 7 refigured from Kovar-Eder & Wójcicki (2001). **a** – apical aperture, **eb** – abruptly elongated fruit base, **h** – harpoon, **lh** – lower horn, **n** – neck, **rl** – reduced lower horn, **s** – scar, **st** – stalk, **t** – tubercle, **tl** – tubercle on abaxial base of lower horn, **tu** – tubercle on abaxial base of upper horn, **uh** – upper horn; scale bar 1 cm

Detailed studies of all specimens from Hinterschlagen indicated that there are nine relatively well preserved ones representing *T. srodoniana* (Fig. 3: 10–18). In the species protologue Wójcicki and Zastawniak (1998) suspected that the scar is hidden in at least a short stalk. The present study has definitely confirmed that the characteristically abruptly narrowed fruit base terminates in a relatively short fragile stalk (Fig. 3: 16, 18). In other specimens its former presence is supported by an irregular scar margin. The confirmation of this feature in well defined *Trapa* species contributes significantly to the evolution of the Trapaceae suggesting a probable evolutionary relation of *Trapa* and *Hemitrapa.* The latter probably constitutes an ancestral morphotype of the family. The only known modern *Trapa* species with a stalked fruit base is *Trapa hyrcana* Woronow, a species endemic to the east Caucasus. However, it represents an evolutionary more advanced morphotype.

The discovery of *T. srodoniana* in the Pannonian of Austria extends its regional distribution considerably and suggests stratigraphic relevance of this species for the late Miocene of at least Central Europe.

T. spectabilis Wójcicki & Kovar-Eder
sp. nov.

Figs 4: 1–26, 5: 1–27

2001 *T. ungeri* Wójcicki & Kovar-Eder/*Trapa srodoniana* Wójcicki – putative hybrids; Kovar-Eder & Wójcicki, p. 234, Pl. 6, figs 7–9.

2003 *T. ungeri* Wójcicki & Kovar-Eder/*Trapa srodoniana* Wójcicki; Wójcicki & Zastawniak, p. 162, Fig. 5g–i.

Holotype (designated here). Coll. file No. NHMW 1988/0138/26 (Figs 4: 15, 5: 11)

Paratypes. Coll. file Nos NHMW 1988/0138/2 (Figs 4: 25, 5: 26, 27), 1988/0138/4 (Figs 4: 14, 5: 24, 25), 1988/0138/5 (Figs 4: 7, 5: 17), 1988/0138/9 (Figs 4: 22, 5: 19), 1988/0138/11 (Figs 4: 20, 5: 15), 1988/0138/12 (Figs 4: 16, 17, 5: 6, 7), 1988/0138/20 (Figs 4: 23, 5: 20, 21), 1988/0138/23A (Figs 4: 13, 5: 10).

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.

Further material. Coll. file Nos NHMW 1988/0138/10, 13 (Figs 4: 18, 5: 14), 1988/0138/14, 15, 16 (Figs 4: 2, 5: 18), 1988/0138/17, 18A,B, 19, 21 (Figs 4: 4, 5: 22), 1988/0138/23B,C,D (Figs 4: 3, 5: 3), 1988/0138/24A (Figs 4: 6, 5: 4), 1988/0138/24B (Figs 4: 11, 5: 12), 1988/0138/25 (Figs 4: 8, 5: 2), 27 (Fig. 4: 5), 1988/0138/28 (Figs 4: 9, 5: 8), 1988/0138/29 (Figs 4: 19, 5: 13), 1988/0138/30 (Figs 4: 1, 5: 1), 1988/0138/31 (Figs 4: 26, 5: 23), 1988/0138/32 (Figs 4: 10, 5: 5), 1988/0138/33 (Figs 4: 12, 5: 9), 1988/0138/34 (Figs 4: 21, 5: 16), 1988/0138/35, 36, 37, 38A,B,C, 39; 1988/0138.

Age. Miocene, Pannonian.

Derivation of the name. From the Latin *spectabilis*, meaning spectacular variability of fruits.

Description. Fruits massive, obtriangular to broadly obtriangular in outline with four horns; fruit (9–)13–32 mm high (including neck), width (8–)23–42 mm (including upper horns); fruit about (0.3–)0.4–0.7 as high as wide; head of the fruit pronounced, its upper end located below the line joining the raised bases of the upper horns; neck well developed 0.5–2.5 mm high or fruit head gradually attenuating into a short conical truncate neck, usually not protruding from the margin of the upper horns; corona lacking; apical aperture (1.5–)2–3 mm in diameter; a ring of upward pointing hairs closing the apical aperture sometimes visible; surface of the fruit head and neck finely ribbed; upper horns widely expanded or slightly upward pointing (90°–65°), narrowly triangular in outline, (8–)9–16 mm long, at least slightly raised at the base, usually with characteristic conical tubercles located abaxially at the base of the horns, tubercles up to 2 mm long, upper horns gradually continuing into thin, re exedly barbed spines (harpoons), up to 13 mm long; presence of mat areas excluded; lower horns solid, narrowly triangular in outline, usually re exed, straight, about (2?–)5–13 mm long, located approximately in 1/3–1/2(3/5) from the fruit base, usually with conical tubercles near the base on the abaxial side, tubercles up to 2 mm long; sometimes a small cavity is developed at the base of the lower horn; frame of the fruit well pronounced with solid tubercles located between the upper and lower horns, tubercles 0.5–4 mm long and up to 3 mm wide near the

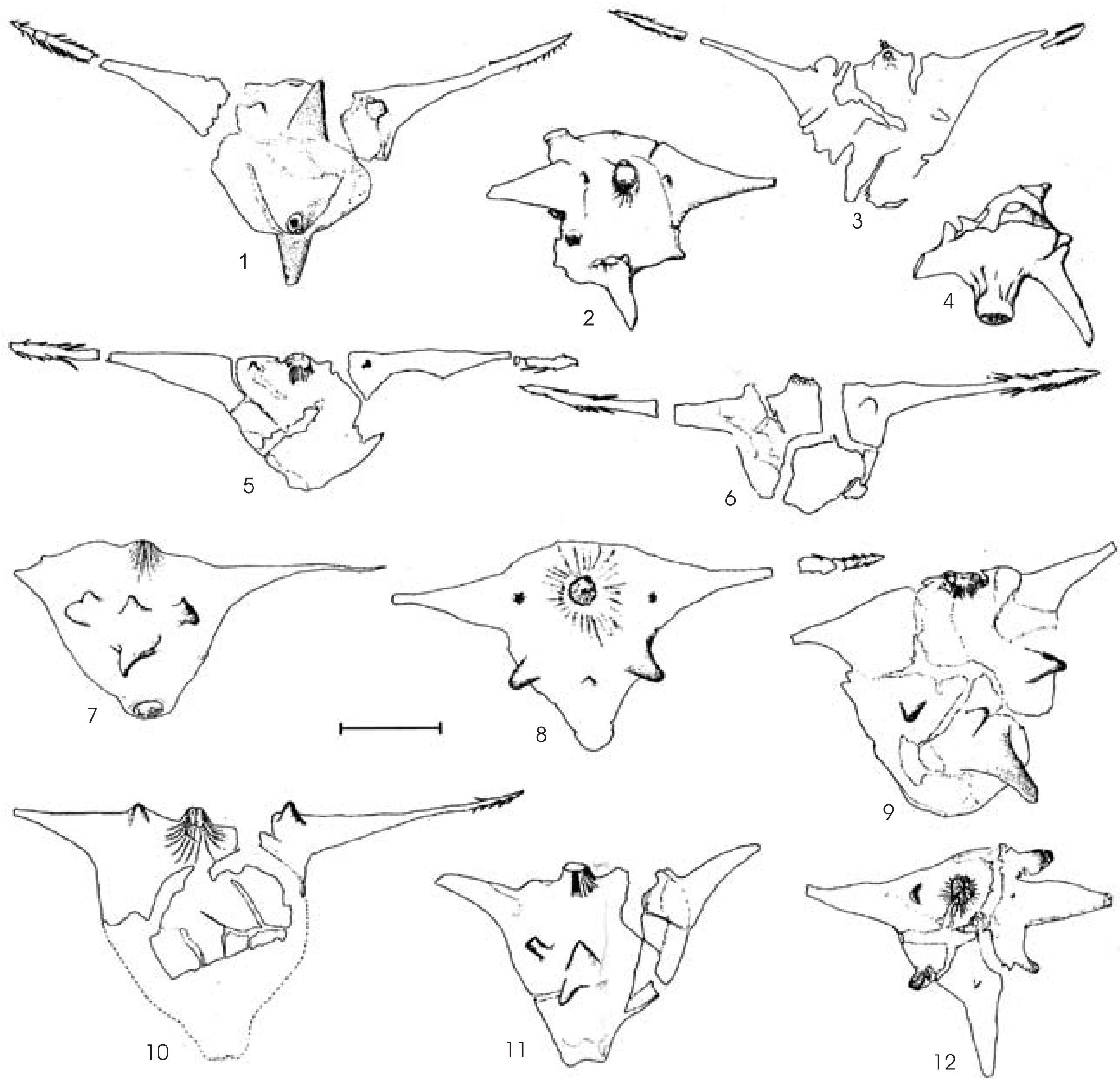
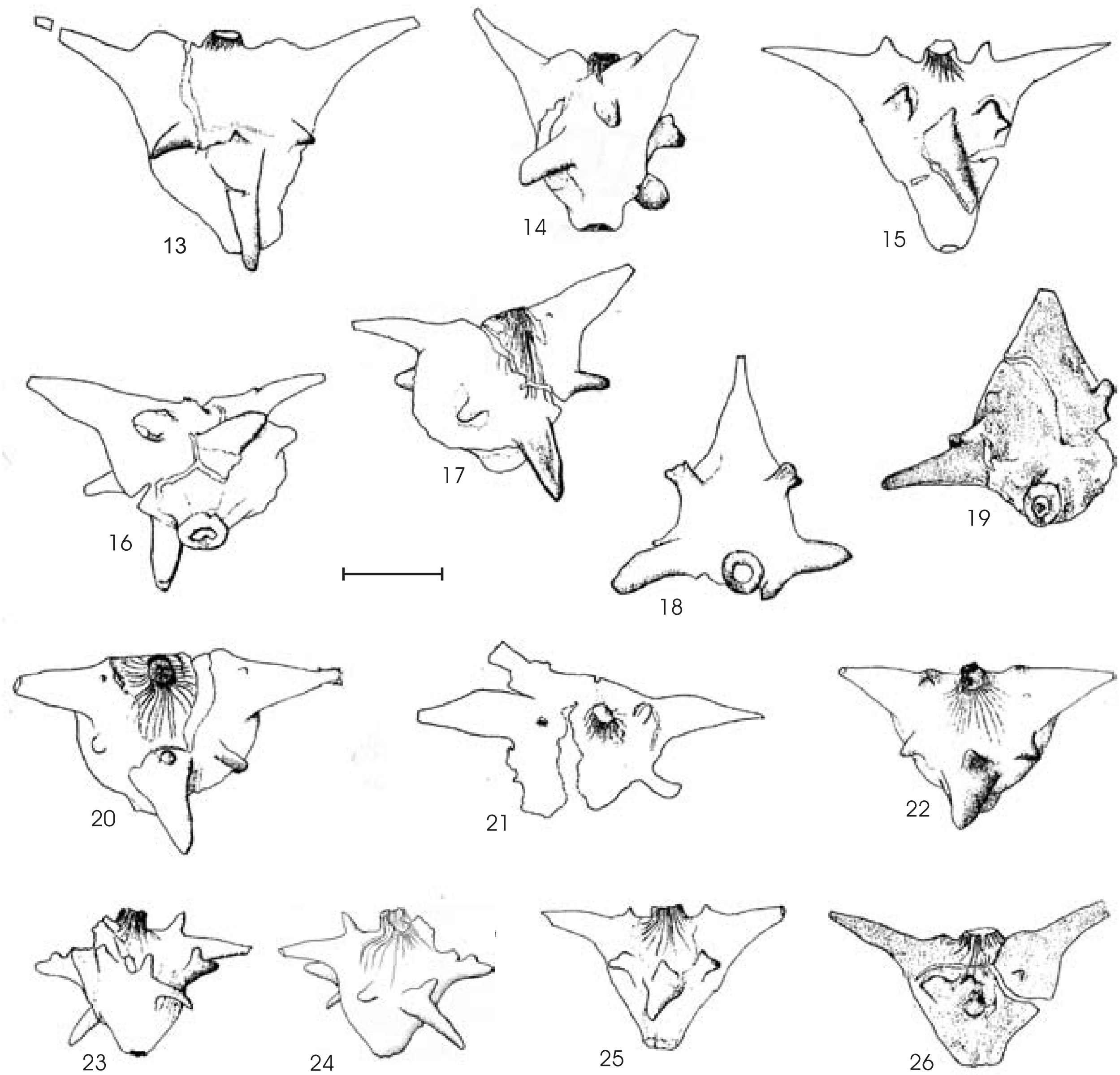


Fig. 4. *Trapa spectabilis* Wójcicki & Kovar-Eder, sp. nov. **1** – No. NHMW 1988/0138/30 (= Fig. 5: 1), **2** – No. NHMW 1988/0138/16 (= Fig. 5: 18), **3** – No. NHMW 1988/0138/23D (= Fig. 5: 3), **4** – No. NHMW 1988/0138/21 (= Fig. 5: 22), **5** – No. NHMW 1988/0138/27, **6** – No. NHMW 1988/0138/24A (= Fig. 5: 4), **7** – No. NHMW 1988/0138/5 (= Fig. 5: 17), **8** – No. NHMW 1988/0138/25 (= Fig. 5: 2), **9** – No. NHMW 1988/0138/28 (= Fig. 5: 8), **10** – No. NHMW 1988/0138/32 (= Fig. 5: 5), **11** – No. NHMW 1988/0138/24B (= Fig. 5: 12), **12** – No. NHMW 1988/0138/33 (= Fig. 5: 9), **13** – No. NHMW 1988/0138/23A (= Fig. 5: 10),

base, sometimes, their upper part is slightly dichotomously forked; basal part of the fruit body obtriangular truncate in outline, sometimes characteristically gently or abruptly narrowed at the base into a thick but smooth, ring-like structure; surface of the basal part of the fruit covered with a few protruding longitudinal ribs; basal scar 1–4 mm in diameter.

Remarks. Part of the rich *Trapa* material from the opencast mine Heissler contains morphotypes that are easily to be classified as *T. ungeri* (Fig. 3: 1–9) and *T. srodoniana* (Fig. 3: 10–18), and several specimens of very variable intermediate morphology (Figs 4, 5; see also Kovar-Eder & Wójcicki 2001). Considering the hybridogenous character of this puzzling group of specimens sharing different combinations of *T. ungeri* and *T. srodoniana* characters we decided to describe it as a new fossil species *T. spectabilis*. Despite similarities to putative parental species, fruits of *T. spectabilis* form a variable but morphologically consistent group characterized e.g. by having an abruptly narrowing



14 – No. NHMW 1988/0138/4 (= Fig. 5: 24, 25), **15** – No. NHMW 1988/0138/26 – holotype (= Fig. 5: 11), **16, 17** – No. NHMW 1988/0138/12 (= Fig. 5: 6, 7), **18** – No. NHMW 1988/0138/13 (= Fig. 5: 14), **19** – No. NHMW 1988/0138/29 (= Fig. 5: 13), **20** – No. NHMW 1988/0138/11 (= Fig. 5: 15), **21** – No. NHMW 1988/0138/34 (= Fig. 5: 16), **22** – No. NHMW 1988/0138/9 (= Fig. 5: 19), **23, 24** – No. NHMW 1988/0138/20 (= Fig. 5: 20, 21), **25** – No. NHMW 1988/0138/2 (= Fig. 5: 26, 27), **26** – No. NHMW 1988/0138/31 (= Fig. 5: 23); 7, 13–17, 20, 22, 23, 25 – paratypes; scale bars 1 cm

broad fruit base with a basal, thick, smooth, and ring-like structure with a regularly rounded margin.

The intermediate character of *T. spectabilis* fruits is especially well expressed in the general fruit shape, which in some specimens corresponds to that of *T. ungeri* (e.g. Fig. 4: 1, 3, 5, 6). The in uence of this putative parent species is especially well pronounced in the presence of conical tubercles developed abaxially at the base of the upper horns in most of the specimens, and solid, apically sometimes dichotomously forked tubercles between the upper and lower horns (e.g. Fig. 4: 7, 14, 15, 18, 23 and Fig. 5: 5, 11, 14, 20). The contribution of *T. srodoniana* is marked in some specimens by a considerable reduction of the lower horns (Fig. 4: 7, 11, 14, 26 and Fig. 5: 5, 12, 23–25) and the shape of the upper part with a well separated neck.

We include into *T. spectabilis* some specimens which are morphologically close to one of the putative parental species and only slightly "polluted" by the other. For example, the specimen NHMW 2001B0010/1 (Fig. 3: 6) included into a row of *T. ungeri* in gross-morphology

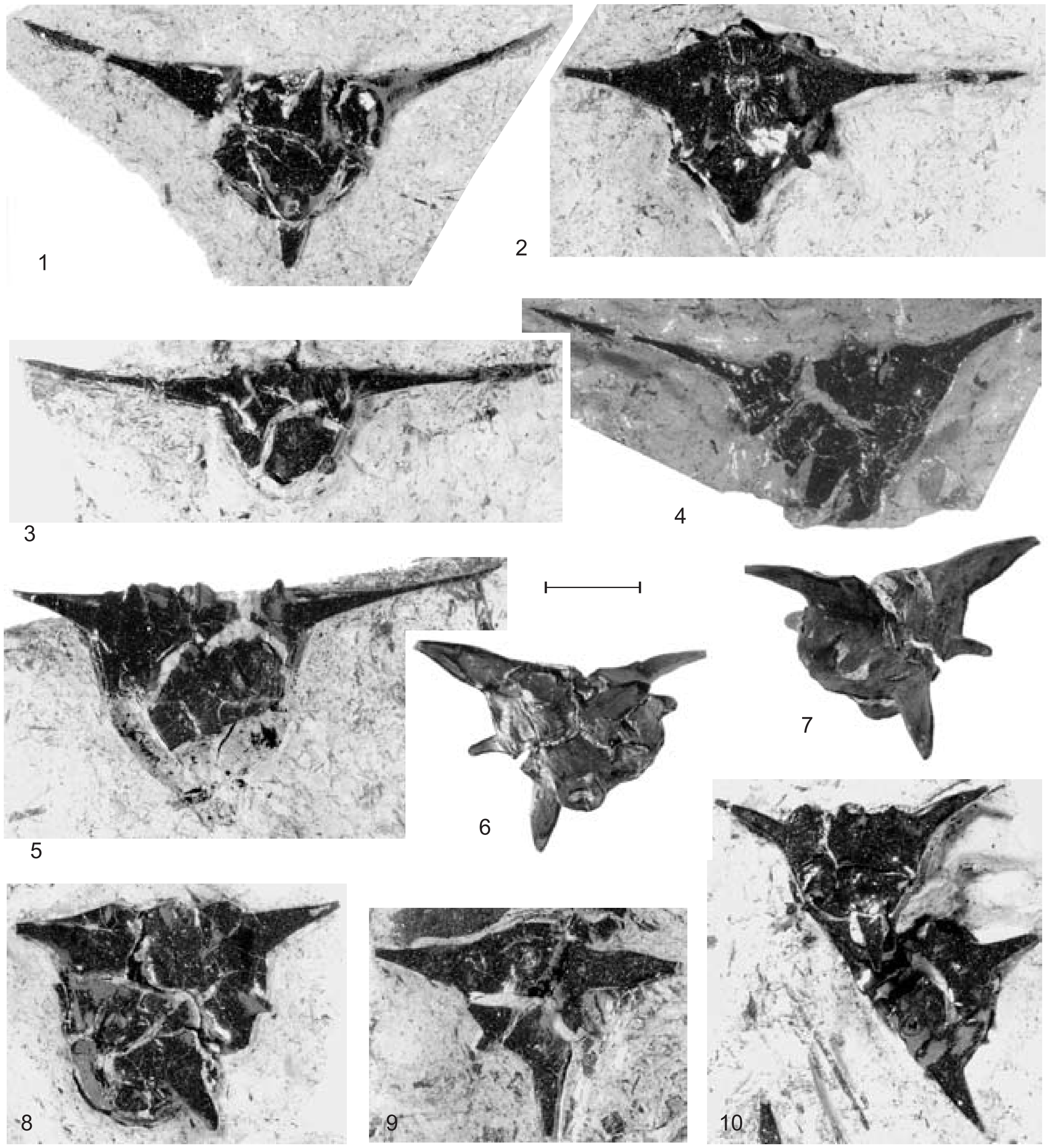
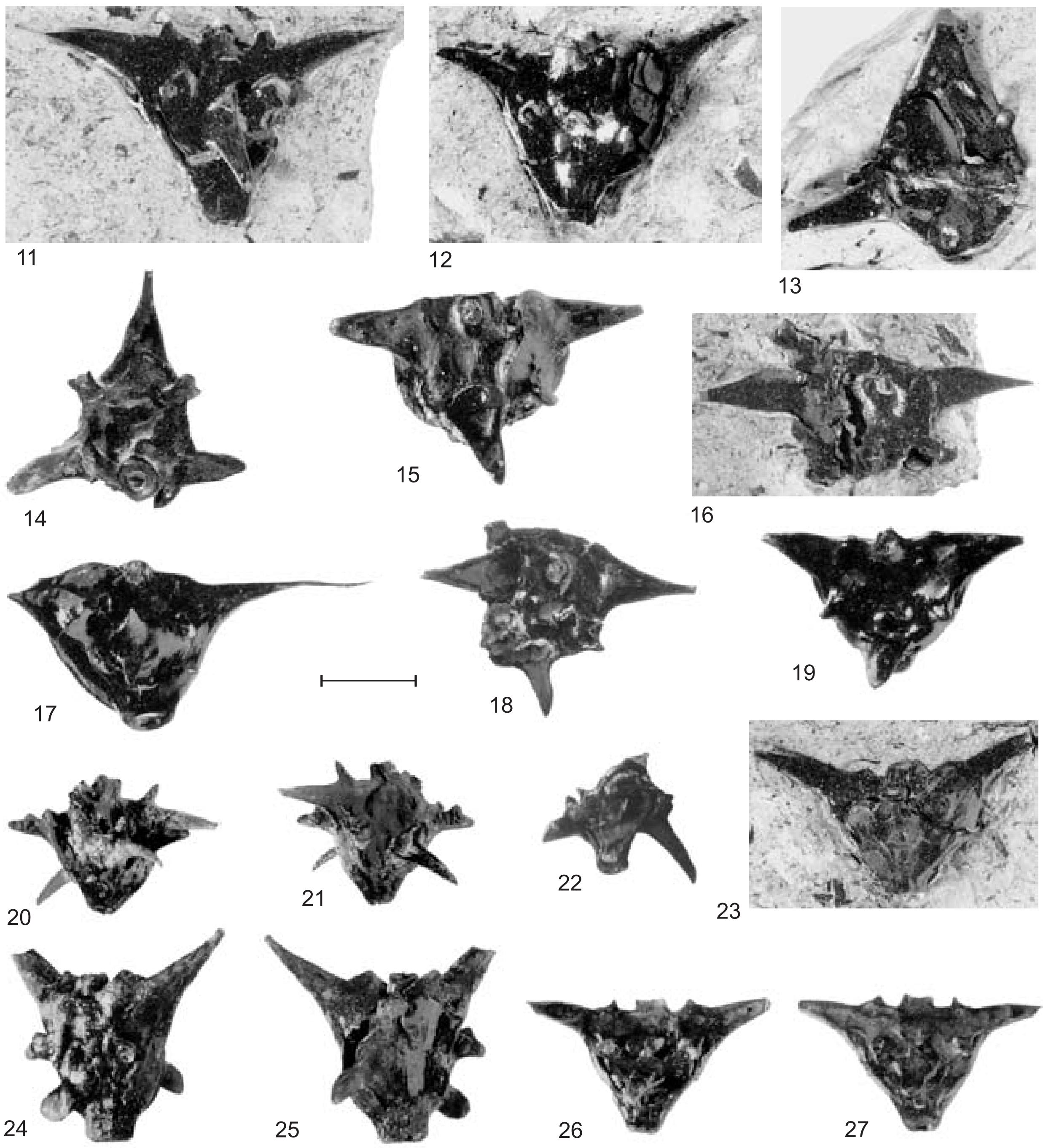


Fig. 5. *Trapa spectabilis* Wójcicki & Kovar-Eder, sp. nov. (**1** – No. NHMW 1988/0138/30 (= Fig. 4: 1), **2** – No. NHMW 1988/0138/25 (= Fig. 4: 8), **3** – No. NHMW 1988/0138/23D (= Fig. 4: 3), **4** – No. NHMW 1988/0138/24A (= Fig. 4: 6), **5** – No. NHMW 1988/0138/32 (= Fig. 4: 10), **6, 7** – No. NHMW 1988/0138/12 (= Fig. 4: 16, 17), **8** – No. NHMW 1988/0138/28 (= Fig. 4: 9), **9** – No. NHMW 1988/0138/33 (= Fig. 4: 12), **10** – No. NHMW 1988/0138/23A, B (= Fig. 4: 13), **11** – No. NHMW 1988/0138/26 – holotype (= Fig. 4: 15), **12** – No. NHMW 1988/0138/24B (= Fig. 4: 11), **13** – No. NHMW 1988/0138/29 (= Fig. 4: 19), **14** – No.

resembles *T. ungeri* but it also resembles *T. srodoniana* by having a stalked base and reduced lower horns. Because of similar morphology this may also concern specimen NHMW 2000B0014/6 (Fig. 3: 8) placed in *T. ungeri*. Such fruit variability as documented from Hinterschlagen seems to be characteristic of a hybrid swarm as recognized in modern *Trapa* (e.g. Staszkiewicz & Wójcicki 1979, Kadono 1987, Tzvelev 1993). The discovery of putative hybrids in the late Miocene supports the suspected presence of hybridization and probable reticulate evolution of the Trapaceae.

In this context, it is noteworthy, that the two specimens known from the Panno-



NHMW 1988/0138/13 (= Fig. 4: 18), **15** – No. NHMW 1988/0138/11 (= Fig. 4: 20), **16** – No. NHMW 1988/0138/34(= Fig. 4: 21), **17** – No. NHMW 1988/0138/5 (= Fig. 4: 7), **18** – No. NHMW 1988/0138/16 (= Fig. 4: 2), **19** – No. NHMW 1988/0138/9 (= Fig. 4: 22), **20, 21** – No. NHMW 1988/0138/20 (= Fig. 4: 23), **22** – No. NHMW 1988/0138/21 (= Fig. 4: 4), **23** – No. NHMW 1988/0138/31 (= Fig. 4: 26), **24, 25** – No. NHMW 1988/0138/4 (= Fig. 4: 14), **26, 27** – No. NHMW 1988/0138/2 (= Fig. 4: 25); 6, 7, 10, 15, 17, 19–21, 24–27 – paratypes; scale bars 1 cm

nian of Odeşti, Romania, originally classified as *Trapa moravica* Opravil & Knobloch (Givulescu & Ţicleanu 1986, Text-fig. 2, Pl. figs 1, 2), are similar to some specimens of *T. spectabilis*. More findings are required to assure, whether the newly described species gave rise to a stabilized morphotype with a distinguished combination of characters and a wider distribution during the Pannonian in at least this part of Europe. Unfortunately, the Romanian material was not available during the visit of the second author to the palaeobotanical collection of the Geological Museum, Bucharest, and, so far, this question remains unsolved.

TRAPACEAE RECORDS FROM AUSTRIA

The early Miocene plant record of Austria is very rich and the middle Miocene one although poorer is still present. However, there are no records of Trapaceae available. Late Miocene (Pannonian) plant assemblages are numerous again. *Trapa* fruits are known by different species (Tab. 1, Fig. 1) from Höllgraben (Pannonian "zone" A/B), Mataschen (Pannonian "zone" B), and Wörth (Pannonian "zone" C; all Styria, Eastern Styrian Basin), from Rohrbach near Ziersdorf (early Pannonian) and Pellendorf (Pannonian "zone" C; both northern margin of the Vienna Basin, Lower Austria), and from Lohnsburg, Großenreith, and Hinterschlagen (Molasse basin, Upper Austria, Pannonian). *Trapa* is also known fom Burghausen/Salzach (Molasse basin, Bavaria, German/Austrian border, ?middle/late Miocene; personal comm. B. Meller, April 2004). *Trapa* pollen (Tab. 1) has been reported from Hinterschlagen, Großenreith (Zetter in Kovar-Eder 1988) and Lukasberg (Upper Austria, middle coal seam of the late Sarmatian/Early–Middle Pannonian sequence; Masselter & Hofmann 2005), from Mataschen (Meller & Hofmann 2004), and Badersdorf (Burgenland, Pannonian "zone" F; Zetter & Ferguson 2001).

In Austria, *Hemitrapa* has only been detected in Pellendorf (*H. trapelloidea* Miki) so far. Contrary to *H. heissigii* Gregor, it is close to the type species described from the Japanese Neogene (Miki 1941, there as Pleistocene, now assigned to the Miocene according to Tsukagoshi et al. 1995, Momohara 1997, Todo Collaborative Research Group 1999). Thus this represents a single spotty occurrence of this Asian species in Europe. Moreover, the co-occurrence of well defined *Trapa* and *Hemitrapa* fruits at Pellendorf is unique in Europe; only from Japan two localities with *Trapa* and *Hemitrapa* in the same horizon are known (Miki 1952). Floating leaves described recently as *Mikia pellendorfensis* from Pellendorf were associated in the levels with *Trapa* and *Hemitrapa* and it is not excluded that they may represent foliage of *Hemitrapa* (for details see Kovar-Eder et al. 2002). Pollen from the same horizon have been investigated only recently by the third author. Contrary to the macro record that yielded exclusively aquatic plants the pollen spectrum contains mainly mesophytic taxa: *Sphagnum*, *Pteris*, *Polypodium*, *Selaginella*, *Picea*, *Abies*, *Pinus haploxylon*, *Pinus diploxylon*, *Cathaya*, *Tsuga*, *Ginkgo*, *Alnus*, *Betula*, *Salix*, *Ulmus, Quercus*, *Trigonobalanopsis*, Ericaceae, *Carya*, *Engelhardia*, Mastixiaceae (*Diplopanax*), *Fraxinus*, Styracaceae (*Rhederodendron*), Rosaceae. Unfortunately, it is bare of both *Trapa* and *Hemitrapa*.

From Rohrbach near Ziersdorf, Pellendorf, Lohnsburg, and Großenreith the specimens are numerous and show relatively small local variation whereas the rich material from Hinterschlagen is extremely variable and may best be explained to represent two species, *Trapa srodoniana* Wójcicki, *T. ungeri* Wójcicki & Kovar-Eder and a hybrid swarm (Kovar-Eder & Wójcicki 2001). This probably hybridogenous morphotype is here described as *T. spectabilis* Wójcicki & Kovar-Eder, sp. nov. (Figs 4, 5).

The regional and stratigraphic clustering of sites re ects favourable sedimentation conditions in the different regions at different times. The plant-bearing sediments represent various facies within uviatile/lacustrine environments. The absence of both *Trapa* and *Hemitrapa* in the Lower and Middle Miocene deposits of Austria cannot be merely assigned to unsuitable facies conditions. With higher probability these observations are stratigraphically relevant, however, the larger geographical aspect is crucial in this respect.

REMARKS ON THE TRAPACEAE IN THE PALAEOGENE AND NEOGENE OF EUROPE (TABLES 3, 4)

FRUITS

Records of *Hemitrapa* are available but scarce from the late Eocene, Kučlín, Bohemia, that indicate some similarity to *H. pomelii* (Boulay) Mai (Wójcicki & Kvaček 2003).

The fruits from Rott, Otterwisch (both late Oligocene) and Rösa-Sausedlitz (early Miocene), Germany, classified by Mai (in Mai & Walther 1991) as *H. pomelii* possess some morphological characters unknown in other fossil and extant members of the family Trapaceae, as e.g. regularly distributed short conical structures inserted laterally on the protruding ribs of the fruit head approximately in its equatorial part. These features

Table 3. Well defined *Trapa* and *Hemitrapa* species from the Miocene and Pliocene of Europe (type or single localities listed only)

Species	Locality	Age	References
T. baasii Gregor & Mehl	Heuchelheim, Germany	Plio-/Pleistocene	Gregor & Mehl 1987
T. bosniaca Janković & Pant*	Tuzla, Bosnia	Late Miocene	Janković & Pantić 19
T. ceretana Rérolle	Sanavastre, La Cerdaña, Spain	Late Miocene, Vallesian (MN 9)	Rérolle 1885, Martin-Closas 1995
T. expectata Givulescu & Ţicleanu	Rovinari, Romania	Pliocene, Romanian	Givulescu & Ţicleanu 1986
T. fritzlariensis Wójcicki & Wilde	Fritzlar, Germany	Pliocene	Wójcicki & Wilde 2001
T. heeri Fritsch	Rippersroda, Germany	Pliocene	Fritsch 1885, Mai et al. 1963
T. moravica Opravil & Knobloch	Moravská Nová Ves, Czech Republic	Miocene, Pannonian	Opravil & Knobloch 1967
T. pellendorfensis Wójcicki & Kovar-Eder	Pellendorf, Austria	Miocene, late Pannonian	Kovar-Eder et al. 2002
T. praehungarica Wójcicki & Baizáth	Bükkábrány, Bükk Mts, Hungary	Miocene, late Pannonian	Wójcicki & Bajzáth 1997
T. silesiaca Göppert emend. Wójcicki & Zastawniak	Sośnica, Poland	Late Miocene/Pliocene	Göppert 1855, Wójcicki & Zastawniak 2002
T. spectabilis Wójcicki & Kovar-Eder	Hinterschlagen, Austria	Miocene, late Pannonian	This paper
T. srodoniana Wójcicki	Bełchatów, Poland	Late Miocene	Wójcicki & Zastawniak 1998
T. strausii Kovar & Gregor	Willershausen, Germany	Late Pliocene	Kovar & Gregor 1984
T. urceolata Givulescu & Ţicleanu	Rovinari, Romania	Pliocene, Romanian	Givulescu & Ţicleanu 1986
T. ungeri Wójcicki & Kovar-Eder	Hinterschlagen, Austria	Miocene, late Pannonian	Kovar-Eder et al. 2002
H. teumeri (Menzel) Budantzev	Großräschen, Germany	Middle Miocene	Menzel 1933, Mai 2001
H. heissigii Gregor	Eberstetten	Early/early Middle Miocene (MN 5-6)	Gregor 1982a
H. pomelii (Boulay) Mai	Gergovie, France	Early Miocene, Burdigalian	Boulay 1899, Mai in Mai & Walther 1991, Wójcicki & Kvaček 2003
H. trapelloidea Miki	Pellendorf, Austria	Miocene, late Pannonian	Kovar-Eder et al. 2002

* including enigmatic *T. pontica*, *T. tuzlensis*, and *T. praemuzzanensis* described by Janković and Pantić (1953) from the same locality

suggest the existence of another independent fruit morphospecies, representing a probably "blind" evolutionary lineage of the family Trapaceae (cf. Wójcicki & Kvaček 2003, Wójcicki & Zastawniak 2003). This problem is subject of ongoing detailed studies by the second author to be presented separately.

Contrary, *H. pomelii* from its type locality in Gergovie, France (Burdigalian; Saporta 1878, Boulay 1899) exhibits a characteristic *Hemitrapa* morphology, as defined by Miki (1941).

Former *Trapa credneri* Schenk from Bohemia and Saxony is an index fossil of the middle Early Miocene Floral Assemblage ("Florenkomplex") Bílina–Brandis sensu Mai (1995). Due to its unique morphology, lacking any modern analogue, it has recently been assigned to the newly created genus *Schenkiella* and, therefore has to be excluded from the Trapaceae (Wójcicki & Kvaček 2002a).

The mass occurrence of *Hemitrapa heissigii* Gregor from the Lom Coal Seam, Lom Formation in North Bohemia (Early Miocene; Wójcicki & Kvaček 2002b) is one of the earliest unambiguous records of this species. Later, especially in MN 5 to MN 6 correlated to the late Early to early Middle Miocene, *H. heissigii* is often specimen-richly represented at numerous localities in the Molasse basin in Bavaria (Gregor 1980, 1982a,b, 1986, Schmid & Gregor 1983, Gregor & Schmid 1983, Günther & Gregor 1989, Riederle & Gregor 1997, Schmitt & Butzmann 1997, Riederle 1997), and Saxony and Brandenburg (Mai 2001, Czaja 2003). So far, we lack evidence of *H. heissigii* from the late Miocene there. The youngest records of *H. heissigii* (although not very characteristic and, therefore, earlier misidentified as *Trapa silesiaca*; e.g. Menzel 1906) have recently been reported from the Lusatia region, Rauno

Sequence. Mai (2001: 112) proposes a late Miocene age of these fruits (Florenzone XIII after Mai 1967). However, this correlation is not clear as Mai (1995: p. 369, 371, Abb. 164) indicates a Middle Miocene age for Florenzone XIII.

Recently, *Trapa fritzlariensis* Wójcicki & Wilde was described (Fritzlar, Hessen, Germany; Pliocene) with a set of characters intermediate between *Trapa* and *Hemitrapa*. The same can be stated for the record figured by Huckriede and Urban (1998: Pl. 5, figs 8 and 9 scale problematic) as *H. heissigii* from the same site, thus expressing the problematic status of the genus *Hemitrapa* from the point of fruit morphology. Intermediate forms between *Hemitrapa* and *Trapa* are also known from some other sites in Germany (e.g. Gr. Kausche, Kleinleipisch, Klettwitz, Rauno, Wischgrund) and, recently, they were included by Mai (2001) into *H. heissigii*. However, this problem is more complex and requires further studies.

An identity of *Hemitrapa teumeri* (Menzel) Budantzev (Menzel 1933, Mai 2001) from the Middle Miocene of Großräschen included here in Table 3 remains problematic as its type material has been destroyed after World War II (see Mai 2001). Nevertheless, the description and iconography provided by Menzel (1933) suggest that it rather should be treated as conspecific with *Hemitrapa trapelloidea* (cf. Kovar-Eder et al. 2002). So far, the only well dated European late Miocene record of *Hemitrapa* is that of *H. trapelloidea* from Pellendorf in Austria (late Miocene, Pannonian "zone" C).

Unambiguous *Trapa* morphotypes have not yet been discovered earlier than the late Miocene. Increasing diversity of *Trapa*, wide distribution, and specimen richness at many localities are characteristic of the European late Miocene and Pliocene; the same phenomenon concerns East Asia (cf. Miki 1952, Wójcicki et al. 1999). Except for *T. silesiaca*, which is known now from many sites (see synonymy above) and *Trapa srodoniana* reported from Austria and Poland, many *Trapa* species do not seem to be widely distributed (*T. ungeri* Wójcicki & Kovar-Eder, *T. spectabilis* Wójcicki & Kovar-Eder sp. nov., *T. pellendorfensis* Wójcicki & Kovar-Eder, *T. praehungarica*

Table 4. Selected European plant sites with records of Trapaceae/possible Trapaceae based on more than a single plant organ

Locality	Age	Pollen	Fruits	Leaves
Pfaffenzell	Miocene, around 14.6 m.a.	*Sporotrapoidites erdtmanii* (Nagy) Nagy	*Hemitrapa heissigii* Gregor	–
Entrischenbrunn	Miocene, MN 5/6	*Sporotrapoidites erdtmanii* (Nagy) Nagy	*Hemitrapa heissigii* Gregor	–
Gallenbach	Middle Miocene	*Sporotrapoidites erdtmanii* (Nagy) Nagy	*Hemitrapa heissigii* Gregor	–
Kreuzau	Late Middle Miocene	*Sporotrapoidites erdtmanii* (Nagy) Nagy	*Hemitrapa* sp.	–
Mataschen	Late Miocene, Pannonian "zone" B	*Trapa* sp.	*Trapa silesiaca* (Göppert) emend. Wójcicki & Zastawniak	
Hinterschlagen	Late Miocene, Pannonian	*Sporotrapoidites illingensis* Klaus	*Trapa srodoniana* *T. ungeri* Wójcicki & Kovar-Eder *T. spectabilis* Wójcicki & Kovar-Eder	–
Lohnsburg	Late Miocene, Pannonian	*Trapa* sp.	*Trapa silesiaca* Göppert emend. Wójcicki & Zastawniak	–
Pellendorf	Late Miocene, Pannonian "zone" C	–	*Hemitrapa trapelloidea* Miki *Trapa pellendorfensis* Wójcicki & Kovar-Eder	*Mikia pellendorfensis* Kovar-Eder & Wójcicki
Sanavestre	Late Miocene, late Vallesian	*Sporotrapoidites carlesii* Zetter & Ferguson	*Trapa ceretana* Rerole	–
Sośnica	Late Miocene	–	*Trapa silesiaca* (Göppert) emend. Wójcicki & Zastawniak	*Trapa assmanniana* (Göppert) Gothan

Wójcicki & Bajzáth, *T. bosniaca* Janković & Pantić along with enigmatic *T. pontica* Janković & Pantić, *T. praemuzzanensis* Janković & Pantić and *T. tuzlensis* Janković & Pantić described from the same locality, *T. ceretana* Rérolle, and *T. moravica* Opravil & Knobloch).

With the exception of *Trapa heeri* Fritsch, and the well known Pliocene taxa (e.g., *T. baasii* Gregor & Mehl., *T. expectata* Givulescu & Ţicleanu, *T. fritzlariensis* Wójcicki & Wilde, *T. strausii* Kovar and *T. urceolata* Givulescu & Ţicleanu) rather restricted geographical distribution seems to be characteristic. These observations may re ect a generic tendency towards endemism.

POLLEN

Pollen grains of Trapaceae are characterized by their unique morphology. Pollen grains of *Trapa* and *Hemitrapa* are well distinguishable (Mohr 1983, Mohr & Gee 1990, Zetter & Ferguson 2001). Sediments containing fruits of *Hemitrapa heissigii* from Kreuzau (North Rhine Westphalia, Germany; Middle Miocene), Pfaffenzell, and Entrischenbrunn (both Bavaria; Middle Miocene) were investigated for pollen. They yielded *Sporotrapoidites erdtmanii*, but lacked any other Trapaceae. Therefore, it may be assumed that *S. erdtmanii* pollen and *Hemitrapa heissigii* fruits were produced by the same plant. *Sporotrapoidites erdtmanii* is distinctly smaller than pollen of *Trapa* (*Sporotrapoidites illingensis* – Hinterschlagen and Badersdorf, Austria; *S. carlesii* – Sanavastre open cast mine, La Cerdanya Basin, Spain, late Vallesian; *S. cesarei* – Gif enga, Piedmont, Italy, Pliocene; Zetter & Ferguson 2001). In Hinterschlagen, *Trapa srodoniana* and *T. ungeri* are known from the pollen-bearing sediments. From Sanavestre *Trapa ceretana* is recorded.

The microstructures and sculptures of the pollen grain wall seen by SEM in *Hemitrapa* and the *Trapa* species are very similar. The features of the crest are of diagnostic value for both genera. In *Sporotrapoidites erdtmanii* the sexine of the crest is smooth, perforate and wrinkled and, especially at the poles, only slightly higher than in the equatorial region. In contrast, the crest in the polar region of *Trapa* (fossil and recent) is much higher than in the equatorial area. In addition, the crest of late Miocene *Trapa* is strongly sculptured: irregularly rugulate in *Sporotrapoidites illingensis* and regularly verrucate in *S. carlesii*. In *S. cesarei* the sexine of the crest is smooth especially in the polar region (Zetter & Ferguson 2001) perforate and twisted, as in most extant *Trapa* species (Ding et al. 1991, Agraval & Ram 1998).

The Miocene species are characterized by a small corpus and a transitional zone with a spongy nexine between the corpus and the expanded crest. Zetter and Ferguson (2001) are able to discern a further evolutionary step in the pollen of *Trapa* during the Pliocene: the expansion of the corpus at the expense of the transitional zone. All modern species of *Trapa* have a large corpus and only a small transitional zone like, e.g. the Pliocene *S. cesarei* from Gif enga.

Hemitrapa (*Sporotrapoidites erdtmanii*) and *Trapa* (*Sporotrapoidites illigensis*, *S. carlesii*, *S. cesarei*) have not yet been encountered together. The sediments bearing *Trapa pellendorfensis* and *Hemitrapa trapelloidea* at Pellendorf although yielding pollen were bare of either *Trapa* and *Hemitrapa* (see chapter "Trapaceae records from Austria").

LEAVES

Contrary to fruits, leaves of Trapaceae are generally extremely rare in the Tertiary of Europe, e.g. *Trapa assmanniana* (Göppert) Gothan in Potonié, one specimen which is lost (Göppert 1855, Wójcicki & Zastawniak 2002). All the more the mass-occurrence of oating leaves described as *Mikia pellendorfensis* Kovar-Eder & Wójcicki from Pellendorf (Kovar-Eder et al. 2002) is remarkable. Due to the lack of double terminal protrusions on the tooth apices and differences in the shape of the blades, these leaves certainly do not represent *Trapa*. Moreover, no modern analogue is known to compare well. Therefore, it is likely (not excluded) that these leaves may represent *Hemitrapa*, because *Trapa pellendorfensis* and *Hemitrapa trapelloidea* do co-occur at Pellendorf (Tabs 1, 4).

ECOLOGY

Zetter and Ferguson (2001, Tab. 2) also dealt with the ecology of *Trapa* and *Hemitrapa*. They were able to discern differences in the associated aquatic taxa. Here we want to add the results from Pellendorf and some other European Miocene localities (Tab. 5). In the Pellendorf assemblage with *Trapa pellendorfensis* and *Hemitrapa trapelloidea* associated, Characeae are richly recorded, while they are lacking in the merely *Trapa* bearing sites. Contrary, the Nymphaeaceae are often found associated with *Trapa* but are absent in assembalges with *Hemitrapa heissigii* and *Sporotrapoidites erdtmanii*.

Further investigations will prove whether these observations are relevant to differentiate fossil aquatic assemblages. Although not determinable to the generic level, the Nymphaeaceae are well documented in Pellendorf in association with *Hemitrapa trapelloidea*

Table 5. Aquatic plants in selected European Neogene assemblages with *Trapa/Hemitrapa*. **D** – diaspores, **L** – leaves, **P** – palynomorphs, **R** – rhizomes (after Zetter & Ferguson 2001, supplemented). **1** – Gallenbach, Germany (Schmid & Gregor 1983, Mohr & Gee 1990), **2** – Pfaffenzell, Germany (Günther & Gregor 1989, Meller pers. comm. 2001), **3** – Entrischenbrunn, Germany (Meller pers. comm. 2001), **4** – Kreuzau, Germany (Ferguson et al. 1998), **5** – Berzdorf, Germany (Czaja 2003), **6** – Badersdorf, Austria (Zetter & Ferguson 2001), **7** – Hinterschlagen, Austria (Zetter & Ferguson 2001, Kovar-Eder & Wójcicki 2001), **8** – Pellendorf, Austria (Kovar-Eder et al. 2002), **9** – Bełchatów, Poland (Wójcicki & Zastawniak 1998), **10** – Sośnica, Poland (Stachurska et al. 1973, Wójcicki & Zastawniak 2002), **11** – Tabaki, Ukraine (Negru 1979), **12** – Gif enga, Italy (Martinetto 1998), **13** – Berezinka, Ukraine (Il'inskaya 1968), **14** – Mataschen, Austria (Meller & Hofmann 2004), **15** – Oberzella, Germany (Gümbel & Mai 2004)

Taxon / Locality	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Aldrovanda											D	D			
Azolla					D	P			D	D	D	P			
Botryococcus						P	P								
Brasenia							D				D				
Ceratophyllum	D	D	D		D		D	L+D			D	D		D	D
Characeae	D	D						D							
Euryale / Eoeuryale / Pseudoeuryale	D	D	D			P	D		D	D	D	D		D	
Hemitrapa	D+P	D+P	D+P	D+P	D			?L+D							
Hydrocharis					D										
Lemnaceae						P	D				D	D			
Lemnospermum					D										
Limnobiophyllum									L	L					
Lobelia															D
Mikia								L							
Myriophyllum						P	P					P		P	
Najas									D		D				
Nelumbo						P	P						L		
Nuphar											D	D+P			D
Nymphaeaceae								R							
Nymphaea						P	D				D			D	
Pediastrum						P	P								
Potamogeton	D+P	D	D		D		D	D	D	P	D	P	D	D	D
Proserpinaca							P		D						D
Ranunculus subgen. *Batrachium*						P	D+P		D	P+D		P			D
Salvinia		L	P	L+P	D				D+L	L	D	P			D
Stratiotes			D	D	D		D			P	D				D
Trapa						P	D+P	D	D	L+D	D	D	D	D+P	D
Trapella											D				
Utricularia							P								
Zygnemataceae						P	P								
Number of taxa	5	6	6	3	8	11	16	7	9	8	14	11	3	6	9

and *Trapa pellendorfensis* thus stressing the peculiarity of this ora. Evidently, even during the Neogene, aquatic associations underwent (stratigraphically relevant) evolutionary changes.

CONCLUSIONS

1. The Trapaceae are known from ten late Miocene localities in Austria (four by fruits, two by pollen, three by fruits and pollen, one by fruits, leaves, and pollen). The fruits are documented by one species of *Hemitrapa* (*H. trapelloidea*) and five of *Trapa* (*T. pellendorfensis, T. silesiaca, T. spectabilis, T. srodoniana, T. ungeri*). The pollen is documented by *Sporotrapoidites illingensis* representing *Trapa*. Leaves probably belonging to the Trapaceae have been described as *Mikia pellendorfensis*.

2. The taxonomic investigations confirmed the occurrence of *Trapa silesiaca* at six localities in Austria. This species was probably most common in the late Miocene of Europe. Obviously, it does not continue into the Pliocene.

3. Numerous extremely variable fruits from Hinterschlagen represent two easily distinguishable species, *Trapa srodoniana* and *T. ungeri*, and an intermediate probably hybridogenous morphotype described here as a new fossil species *T. spectabilis* Wójcicki & Kovar-Eder, sp. nov. The observed fruit variability at Hinterschlagen seems characteristic of a hybrid swarm. The presence of putative hybrids in the Neogene leads us to the interpretation that hybridization was an essential factor in diversity/speciation of the Trapaceae.

4. The rather restricted geographical distribution of many Miocene and Pliocene species may re ect a family/generic tendency towards endemism.

5. The confirmation of the presence of a stalked base in *Trapa srodoniana* fruits which is also a characteristic feature of the genus *Hemitrapa* serves as additional argument that the *Hemitrapa*-morphotype was probably ancestral to *Trapa*.

6. The stratigraphic value of Trapaceae fruits depends on the precise differentiation at species level. Detailed taxonomic investigations of the European record are still in progress. However, the here presented results suggest that at least some, if not most, species possess stratigraphic relevance. Due to probable family/generic tendency towards endemism the stratigraphic value of single taxa may be regionally limited.

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REFERENCES

AGRAVAL A. & RAM H.Y.M. 1998. Pollen dimorphism in *Trapa* (Trapaceae) from India. Phytomorphology, 48(3): 295–302.

BOULAY J.N. 1899. Flore fossile de Gergovie. Ann. Soc. Sci. Bruxelles, 23: 55–132.

ĆORIĆ S., HARZHAUSER M., HOHENEGGER J., MANDIC O., PERVESLER P., ROETZEL R., RÖGL F., SCHOLGER R., SPEZZAFERRI S., STINGL K., ŠVABENICKÁ L., ZORN I. & ZUSCHIN M. 2004. Stratigraphy and correlation of the Grund Formation in the Molasse basin, Northeastern Austria (Middle Miocene, Lower Badenian). Geologica Carpathica, 55(2): 207–215.

CZAJA A. 2003. Paläokarpologische Untersuchungen von Taphozönosen des Unter-und Mittelmiozäns aus dem Braunkohlentagebau Berzdorf/Oberlausitz (Sachsen). Palaeontographica, B, 265: 1–148.

DING B., FANG Y., ZHANG H., LIANG H. & ZHAO L. 1991. Studies on the pollen morphology of *Trapa* from Zhejiang. Acta Phytotax. Sin., 29: 172–177.

FERGUSON D.K., PINGEN M., ZETTER R. & HOFMANN C.-C. 1998. Advances in our knowledge of the Miocene plant assemblage from Kreuzau, Germany. Rev. Palaeobot. Palynol., 101: 147–177.

FRITSCH K., von 1885. Das Pliozän im Thalgebiete der zahmen Gera in Thüringen. Jahrb. König. Preuss. Geol. Landesanst. Bergakad. Berlin, (1884): 388–437.

GIVULESCU R. & ŢICLEANU N. 1986. Fossile *Trapa*-Früchte aus Rumänien. Dări de Seam ale Şedinţelor, 3. Paleontologie, [1983, 1984], 70–71(3): 187-193.

GÖPPERT H.R. 1852. Ueber die Braunkohle des nordöstlichen Deutschlands. Z. Deutschen Geolog. Ges., 4: 484–496.

GÖPPERT H.R. 1855. Die tertiäre Flora von Schossnitz in Schlesien. Heyn'sche Buchhandlung (E.Remer), Görlitz.

GREGOR H.-J. 1980. Die miozänen Frucht- und Samen-Floren der Oberpfälzer Braunkohle. 2. Funde aus den Kohlen und tonigen Zwischenmitteln. Palaeontographica, B, 174: 7–94.

GREGOR H.-J. 1982a. Fruktifikationen der Gattung *Hemitrapa* Miki (Trapellaceae) in den Ablagerungen der Oberen Süßwasser-Molasse Bayerns (mit Bemerkungen zu den fossilen Vorkommen Eurasiens). Feddes Repert., 93(5): 351–358.

GREGOR H.-J. 1982b. Die jungtertiären Floren Süddeutschlands. Paläokarpologie, Phytostratigraphie, Paläoökologie, Paläoklimatologie. F. Enke Verlag, Stuttgart.

GREGOR H.-J. 1986. Neufunde aus der Brackwasser-Molasse Süddeutschlands. Ber. Naturwiss. Vereins Schwaben, 90(2): 55–62.

GREGOR H.-J. & MEHL J. 1987. Pflanzenreste und ein Massenvorkommen von Nüssen der *Trapa baasii* nov. spec. im Plio-Pleistozän der Wetterauer Braunkohle. Documenta Naturae, 36: 1–10.

GREGOR H.-J. & SCHMID W. 1983. Ein Massenvorkommen von *Hemitrapa heissigii* – Früchten (Trapaceae) in der Sondermüll-Deponie Gallenbach bei Dasing (LKrs. Aichach-Friedberg). Ber. Naturwiss. Vereins Schwaben, 87(3/4): 63–69.

GÜMBEL F. & MAI D.H. 2004. Neue P anzenfunde aus dem Tertiär der Rhön. – Teil 2: Pliozäne Fundstellen. Mitt. Mus. Naturk. Berlin, Geowiss. Reihe, 7: 175–220.

GÜNTHER T. & GREGOR H.-J. 1989. Computeranalyse neogener Frucht- und Samen oren Europas, Band 1: Fundorte und deren Florenlisten. Documenta Naturae, 50: 1–180.

HARZHAUSER M., DAXNER-HÖCK G. & PILLER W.E. 2004. An integrated stratigraphy of the Pannonian (Late Miocene) in the Vienna Basin. Austrian Journ. Earth Sci., 95/96: 6–19.

HUCKRIEDE R. & URBAN B. 1998. Ein landschafts- und ußgeschichtlich wichtiges Pannon- bis Altquartär-Profil bei Fritzlar/Hessen. Z. Deutschen Geolog. Ges, 149(1): 105–126.

IL'INSKAYA I.A. 1968. Neogenovye flory Zakarpatskoy USSR (summary: Neogene oras of the Transcarpathian region of the U.S.S.R). Izdatel'stvo Nauka, Leningrad.

JANKOVIČ M. & PANTIČ N. 1953. Fossilarten der Gattung *Trapa* L. in Nord-Ost-Bosnien. Ann. Geolog. Penins. Balcan., 21: 133–142.

KADONO Y. 1987. A preliminary study on the variation of *Trapa* in Japan. Acta Phytotax. Geobot., 38: 199–210.

KOVAR J. 1979. P anzenreste aus dem Pannon (Obermiozän) von Rohrbach bei Ziersdorf (Niederösterreich). Beitr. Paläont. Österreichs, 6: 107–117.

KOVAR J. 1987. Erste Ergebnisse vergleichender oristischer Untersuchungen an mittel- und ober-miozänen Floren der Molassezone nördlich der Alpen und des Pannonischen Sees (Wiener Becken und angrenzende Gebiete). Courier Forsch.-Inst. Senckenberg, 86(1986): 205–217.

KOVAR J. & GREGOR H.-J. 1984. Eine neue ober-pliozäne *Trapa*-Art. Aus den Willershausener Seeablagerungen (Niedersachsen, BRD). Ann. Naturhist. Mus. Wien, 86(A): 63-70.

KOVAR-EDER J. 1988. Obermiozäne (Pannone) Floren aus der Molassezone Österreichs. Beitr. Paläont. Österreich, 14: 19–121.

KOVAR-EDER J. & KRAINER B. 1988. Die Flora und Fazies des Fundpunktes Höllgraben südöstlich von Weiz, Unterpannonium, Steirisches Becken. Mitt. Abt. Paläont. Landesmus. Joanneum, 41: 27–51.

KOVAR-EDER J. & KRAINER B. 1990. Faziesentwicklung und Florenabfolge des Aufschlusses Wörth bei Kirchberg/Raab (Pannon, Steirisches Becken). Ann. Naturhist. Mus. Wien, 91A: 7–38.

KOVAR-EDER J. & WÓJCICKI J.J. 2001. A Late Miocene (Pannonian) ora from Hinterschlagen, Hausruck lignite area, Upper Austria. Acta Palaeobot., 41(2): 221–251.

KOVAR-EDER J., SCHWARZ J. & WÓJCICKI J.J. 2002. The predominantly aquatic ora from Pellendorf, Lower Austria, Late Miocene, Pannonian – a systematic study. Acta Palaeobot., 42(2): 125–151.

KRAJEWSKA K. 1998. Neogene leaf ora from Gnojna (Opole Prov., SW Poland). Acta Palaeobot., 38(1): 25–85.

KRÄUSEL R. 1920. Nachträge zur Tertiär ora Schlesiens. 1. Jahrb. Preuss. Geol. Landesanst., 39(1): 329–433.

MAI D.H. 1967. Die Florenzonen, der Florenwechsel und die Vorstellungen über den Klimaablauf in Jungtertiär der Deutschen Demokratischen Republik. Abh. Zentr. Geol. Inst., Berlin, 10: 55–81.

MAI D.H. 1995. Tertiäre Vegetationsgeschichte Europas. Gustav Fischer Verlag, Jena, Stuttgart, New York.

MAI D.H. 2001. Die mittelmiozänen und obermiozänen Floren aus der Meuroer und Raunoer Folge in der Lausitz. 2. Teil: Dicotyledonen. Palaeontographica, B, 257: 35–174.

MAI D.H. & WALTHER H. 1991. Die oligozänen und untermiozänen Floren Nordwest-Sachsens und des Bitterfelder Raumes. Abh. Staatl. Mus. Mineral. Geol. Dresden, 38: 1–230.

MAI D.H., MAJEWSKI J. & UNGER K.P. 1963. Pliozän und Altpleistozän von Rippersroda in Thüringen. Geologie, 12(7): 765–815.

MARTIN-CLOSAS C. 1995. Plant taphonomy of La Cerdanya Basin (Vallesian, Eastern Pyrenees). Geobios, 18: 287–298.

MARTINETTO E. (ed.) 1998. Pliocene plants, environments and climate of north-western Italy. Guide to the field conference Mottalciata, Bella, Italy. Dipartimento di Scienze della Terra, Torino.

MASSELTER T. & HOFMANN C.-C. 2005. Palynology and palynofacies of Miocene coal-bearing (clastic) sediments of the Hausruck area (Austria). Geobios, 38: 127–138.

MELLER B. & HOFMANN C.-C. 2004. Paläoökologische Interpretation von Diasporen- und Palynomorphen-Vergesellschaftungen aus obermiozänen Seesedimenten (Mataschen bei Fehring, Oststeiermark, Österreich). Joannea Geol. Paläont., 5: 177–217.

MENZEL P. 1906. Über die Flora der Senftenberger Braunkohlen-Ablagerungen. Abh. König. Preuß. Geol. Landesanst., Neue Folge, 46: 1–176.

MENZEL P. 1933. Neues zur Tertiär ora der Niederlausitz. Arb. Inst. Paläobot. Petrogr. Brennsteine, 3(1): 1–43.

MEYER F. 1919. Salicaceen, Aceraceen und die übrigen nachgewiessen P anzenreste. In: Kräusel R. (ed.) Die P anzen des schlesischen Tertiärs. Jahrb. Preuss. Geol. Landesanst., 38(2): 145–190.

MIKI S. 1941. On the change of ora in Eastern Asia since Tertiary period (1). The clay or lignite beds ora in Japan with special reference to the *Pinus trifolia* beds in Central Hondo. Jap. J. Bot., 11: 237–303.

MIKI S. 1952. *Trapa* of Japan with special reference to its remains. J. Inst. Polytechn., Osaka City Univ., Ser. D, 3: 1–30.

MOHR B.A.R. 1983. Nachweis von Pollen der Gattung *Hemitrapa* Miki (Trapaceae) aus mittelmiozänen Schichten von Gallenbach bei Dasing (Lkrs. Aichach-Friedberg). Ber. Naturwiss. Vereins Schwaben, 87(3/4): 69–72.

MOHR B.A.R. & GEE C.T. 1990. *Sporotrapoidites erdtmanii* (Nagy) Nagy, a trapaceous pollen species pertaining to the Oligocene to Pliocene genus *Hemitrapa* Miki. Grana, 29: 285–293.

MOMOHARA A. 1997. Cenozoic history of evergreen broad-leaved forest in Japan. Nat. Hist. Res., Special Issue, 4: 141–156.

NEGRU A. G. 1979. Ranneponticheskaya flora yuzhnoy chasti dnestrovsko-prutskovo mezhdurech`ya. Shtiintza, Kishinev.

OPRAVIL E. & KNOBLOCH E. 1967. *Trapa moravica* spec. nova – eine neue Wassernuss aus dem Pannon des Wiener Beckens. Preslia, 39: 117–121.

RÉROLLE L. 1885. Végétaux fossiles de Cerdagne. Rev. Sci. Nat., Montpellier, 3 sér., 4(1884–1885): 167–386.

RIEDERLE R. 1997. Die Sandgrube Ursberg bei Thannhausen – Stratigraphie einer neuen miozänen Fundstelle aus der Molasse Bayerisch-Schwabens. Documenta Naturae, 110: 103–118.

RIEDERLE R. & GREGOR H.-J. 1997. Die Tongrube Kirrberg bei Balzhausen – eine neue Fundstelle aus der Oberen Süßwassermolasse Bayerisch-Schwabens – Flora, Fauna, Stratigraphie. Documenta Naturae, 110: 1–53.

SAPORTA G. 1878. Essai descriptif sur les plantes fossils des arkoses de Brives. Ann. Soc. Agric. Sci. Arts Comm. Puy, 33: 1–72.

SCHMID W. & GREGOR H.-J. 1983. Gallenbach - eine neue mittelmiozäne Fossilfundstelle in der westlichen Oberen Süßwassermolasse Bayerns. Ber. Naturwiss. Vereins Schwaben, 87(3/4): 51–63.

SCHMITT H. & BUTZMANN R. 1997. Entrischenbrunn – Statistische Untersuchungen an einer neuen Florenfundstelle aus der Oberen Süßwassermolasse im Landkreis Pfaffenhofen a.d.Ilm. Documenta Naturae, 110: 55–87.

STACHURSKA A., SADOWSKA A. & DYJOR S. 1973. The Neogene ora at Sośnica near Wrocław in the light of geological, and palynological investigations. Acta Palaeobot., 14(3): 147–176.

STASZKIEWICZ J. & WÓJCICKI J.J. 1979. Analiza biometryczna orzechów rodzaju *Trapa* L. z Polski (summary: Biometrical analysis of *Trapa* L. nuts from Poland). Fragm. Flor. Geobot., 25(1): 33–59.

STASZKIEWICZ J. & WÓJCICKI J.J. 1981. Variability of the metrical characters of nuts of the genus *Trapa* L. from Central Europe. Fragm. Flor. Geobot., 27(3): 415–431.

STUCHLIK L., SZYNKIEWICZ A., ŁAŃCUCKA-ŚRODONIOWA M. & ZASTAWNIAK E. 1990. Wyniki dotychczasowych badań paleobotanicznych trzeciorzędowych węgli brunatnych złoża “Bełchatów” (summary: Results of the hitherto palaeobotanical investigations of the Tertiary brown coal bed “Bełchatów” (Central Poland). Acta Palaeobot., 30 (1,2): 259–305.

SZYNKIEWICZ A. 2000. Wiek węgla brunatnego na tle pozycji geologicznej badanych próbek – KWB “Bełchatów” (summary: Age of the brown coal deposits from the Bełchatów lignite mine, Central Poland). Przegląd Geologiczny, 48(11): 1038–1044.

TODO COLLABORATIVE RESEARCH GROUP 1999. Fault bounded inland basin of multiple bloks: an example from the sedimentary basin of the Tokai Group around Tajimi City in Gifu Prefecture, central Japan. Earth Science (Chikyu Kagaku), 53: 291–306 (in Japanese with English summary).

TSUKAGOSHI M. & TODO COLLABORATIVE RESEARCH GROUP 1995. Plant megafossils from the Pliocene Toki Sand and Gravel Formation in and around Ena City, Gifu Prefecture, central Japan. Bull. Osaka Mus. Nat. Hist., 49: 23–46.

TZVELEV N.N. 1993. O rode *Trapa* L. (Trapaceae) v vostochnoy Evrope i severnoy Azii (De genere *Trapa* L. (Trapaceae) in Europa orientali et Asia Boreali). Novosti Sistematiki Vysshikh Rasteny, 29: 99–107. (in Russian).

VASSILEV V.N. 1973. Novye vidy vodyanovo orekha – *Trapa* L. (Generis *Trapa* L. species novae). Novosti Sistematiki Vysshikh Rasteny, 10: 175–194. (in Russian).

WÓJCICKI J.J. & BAJZÁTH J. 1997. *Trapa praehungarica*, a new fossil species from the Upper Pannonian of Hungary. Acta Palaeobot., 37(1): 51–54.

WÓJCICKI J.J. & KVAČEK Z. 2002a. *Schenkiella* genus novum, thorny disseminules of unknown affinities from the Lower Miocene of Central Europe. Acta Palaeobot., 42(2): 109–116.

WÓJCICKI J.J. & KVAČEK Z. 2002b. *Hemitrapa* fuits (Trapaceae) in the late Early Miocene Lom Coal Seam, Most Formation, North Bohemia. Acta Palaeobot., 42(2): 117–124.

WÓJCICKI J.J. & KVAČEK Z. 2003. The earliest fossil record of the *Trapaceae* in Europe from the Late Eocene diatomite of Kučlín, north Bohemia. Phytologia Balcanica, 9(2): 165–174.

WÓJCICKI J.J. & WILDE V. 2001. A new species of *Trapa* (Trapaceae) from the Pliocene of the Zennern Depression, near Fritzlar (Hesse, Germany). Senckenbergiana Lethaea, Frankfurt/Main, 81(1): 17–23.

WÓJCICKI J.J. & ZASTAWNIAK E. 1998. *Trapa srodoniana*, a new fossil species from the Pliocene of Bełchatów (Middle Poland). Acta Palaeobot., 38(1): 167–174.

WÓJCICKI J.J. & ZASTAWNIAK E. 2002. Late Miocene *Trapa* L. of Sośnica (SW Poland) revisited. Acta Palaeobot., 42(1): 29–38.

WÓJCICKI J.J. & ZASTAWNIAK E. 2003. Rodzina Trapaceae w trzeciorzędzie Europy – wstępne wyniki badań (summary: The Trapaceae family in the Tertiary of Europe – preliminary results). Botanical Guidebooks, 26: 153–185.

WÓJCICKI J.J., SONG S. & WANG Y. 1999. Fossil *Trapa* L. of China. 1. A new locality from the Miocene of the Liang He coal mine, West Yunnan. Acta Palaeobot., 39(1): 5–14.

ZASTAWNIAK E., ŁAŃCUCKA-ŚRODONIOWA M., BARANOWSKA-ZARZYCKA Z., HUMMEL A. & LESIAK M. 1996. Flora megasporowa, liściowa i owocowo-nasienna: 857–932. In: Malinowska L. & Piwocki M. (eds) Budowa geologiczna Polski. Tom 3. Atlas skamieniałości przewodnich i charakterystycznych, 3a, Kenozoik, Trzeciorzęd, Neogen. Polska Agencja Ekologiczna, Warszawa.

ZETTER R. & FERGUSON D.K. 2001. Trapaceae pollen in the Cenozoic. Acta Palaeobot., 42(1): 321–339.