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Late Miocene *Trapa* L. (Trapaceae) of Sośnica (SW Poland) revisited

JAN J. WÓJCICKI and EWA ZASTAWNIAK

W. Szafer Institute of Botany, Polish Academy of Sciences, Lubicz 46, 31-512 Kraków, Poland,
e-mail: wojcicki@ib-pan.krakow.pl; E.Zastaw@ib-pan.krakow.pl

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ABSTRACT. Fossil fruits of *Trapa* from the Late Miocene sediments of Sośnica (SW Poland), described by Goeppert as *Trapa silesiaca* and *T. bifrons*, are revised and re-illustrated. The discovery of additional morphological features has enabled a precise characterization of *T. silesiaca* to be realized with resultant emendation of its diagnosis. The lectotype of *T. silesiaca* is formally designated and an epitype selected for the purpose of providing a precise application of the name *T. silesiaca*. Studies of specimens from the original collection determined by Goeppert as *T. bifrons* confirmed earlier suggestions that this species is conspecific with *T. silesiaca*. The correct citation of *Trapa assmanniana* (Goeppert) Gothan in Potonié described and illustrated by Goeppert from Sośnica as *Populus assmanniana* is provided. The taphocoenosis of fossil plants from Sośnica is also briefly characterized.

KEY WORDS: fossil fruit, *Trapa*, morphology, taxonomy, lectotypification, emendation of diagnosis, Neogene, Europe

INTRODUCTION

Tertiary fruits of *Trapa* L. (Trapaceae) were first recognized and named by Goeppert (1852, 1855) in a Miocene flora from Sośnica near Wrocław (SW Poland). The *Trapa* fossils were accompanied by numerous plant remains preserved as impressions of leaves, fruits, seeds, flowers and inflorescences belonging to many fossil taxa. He later described and illustrated the material in a comprehensive monograph (Goeppert 1855) which was the first monograph of a Miocene flora. This book contains descriptions of many new fossil species, including two of *Trapa* – *T. silesiaca* and *T. bifrons*. Menzel (1906) was the first who noted that in fact *T. bifrons* does not essentially differ from *T. silesiaca* and should be synonymized with it. The specific name *T. silesiaca* was subsequently used by several authors for fossil fruits of *Trapa* from other European Neogene localities (e.g. Heer 1881, Boulay 1890, Menzel 1906, Kräusel 1920, Depape 1922, Menzel et al. 1933, Kirchheimer 1937, 1957, Szafer 1954, Raniecka-Bobrowska 1954, 1959, Kilpper 1959, Hurník 1961, Mai 1963, 1989, Kramer 1974, Gregor 1980, Kovar-Eder & Krainer 1990, Stuchlik et al. 1990, Krajewska 1998). In some cases, however, the fruits represented some other fossil taxa (cf. Gregor 1982, Wójcicki & Zastawniak 1998, Mai 2001). Critical reinvestigation of Goeppert's original collection and the relatively copious additional material collected subsequently from Sośnica (Łańcucka-Środoniowa et al. 1981) has enabled a detailed characterization of the variability of *T. silesiaca* and emendation of its diagnosis.

In his monograph, Goeppert (1855) also described and illustrated a single leaf as *Populus assmanniana*. The affinity of this specimen with *Trapa* seems to be evident, as has been discussed by Nathorst (1884), Rérolle (1885), Boulay (1890), Menzel (1906) and Meyer (1913, 1919). According to these authors, however, the species is synonymous with *Trapa silesiaca* Goeppert. In our opinion it should be treated as a separate fossil species because the leaf was found detached from the fossil fruit. Gothan (in Potonié 1921) was the first author

who made a valid combination of this fossil species. The correct citation of it is *Trapa assmanniana* (Goeppert) Gothan in Potonié, Lehrbuch der Palaeobotanik: 394, Fig. 316(3). 1921 (see also Palibin & Krishtofovich 1956). Unfortunately, the holotype of *T. assmanniana* was lost before the beginning of the 20th century (cf. Meyer 1919) and a more detailed characterization of this species is not possible, because no other material of this kind is available.

The present paper is a continuation of subsequent revisions of the flora of Sośnica (Łańcucka-Środoniowa et al. 1981, Walther & Zastawniak 1991, Zastawniak et al. 1996, Zastawniak & Walther 1998, Collinson et al. 2001) as well as a further contribution to a taxonomic project on the Tertiary *Trapa* of Europe (Wójcicki & Bajzath 1997, Wójcicki & Zastawniak 1998, Kovar-Eder & Wójcicki 2001, Wójcicki & Wilde 2001, Kovar-Eder et al. submitted).

MATERIAL AND METHODS

The fossil specimens of *Trapa* used for this study came from four palaeobotanical collections. In Goeppert's original collection housed in the Geological Museum of the Institute of Geological Sciences of the University of Wrocław (MGUWr) the specimens are preserved as impressions and, in most cases, Goeppert's original labels are attached to the specimens. The remaining three collections belong respectively to the palaeobotanical collection of the W. Szafer Institute of Botany of the Polish Academy of Sciences in Kraków (KRAM-P), the Natural History Museum, Berlin (MfN) and the Museum of the Earth, Polish Academy of Sciences, Warsaw (MZ), where the material is preserved as impressions and/or oxidized compressions of fruits. Macrophotography was carried out using Kodak Academy (200 ASA) film, a Minolta X700 camera with 1:1 Kenko converter and Minolta Rokkor-X 50 mm lens. For an analysis of the growth forms of the Sośnica taphocoenosis the method suggested by van der Burgh (1994) was used.

SYSTEMATICS

Trapaceae Doum. nom. conserv.

Trapa L.

Trapa silesiaca Goeppert emend. Wójcicki & Zastawniak

Figs 1 & 2

1852 *Trapa silesiaca* Goepp. nom. nud.; Goeppert, p. 495.
1852 *Trapa bifrons* Goepp. nom. nud.; Goeppert, p. 495.
1855 *Trapa silesiaca* Goepp.; Goeppert, p. 38, Pl. 25, fig. 14.
1855 *Trapa bifrons* Goepp.; Goeppert, p. 38, Pl. 25, fig. 15.
1919 *Trapa silesiaca* Goepp.; Meyer, p. 174, Pl. 15, fig. 6 & 7.
1920 *Trapa silesiaca* Goepp.; Kräusel, p. 384, Pl. 23, fig. 27 & 31.
1973 *Trapa kräuselii* V.N. Vassil. sp. nov.; Vassilev, p. 210, Fig. 1: 12.
1996 *Trapa silesiaca* Goepp.; Zastawniak et al., p. 901, Pl. 299, fig. 13.
2001 *Trapa silesiaca* Goepp.; Wójcicki & Wilde, p. 20, Fig. 3a, b.

Lectotype (designated here). Goeppert's collection: MGUWr 812p; Figs 1: 1 & 2: 1.

Epitype (designated here). KRAM-P 54/286 (specimen designated as neotype of *T. silesiaca* Goepp. by Zastawniak et al. 1996: Pl. 299, fig. 13) and KRAM-P 54/285 (counterpart of KRAM-P 54/286); Figs 1: 12 & 2: 5, 6.

Further material. Goeppert's collection: MGUWr 656p/1, 656p/2, 656p/3, 814p (syntypes of *T. bifrons*), 511p (six specimens poorly preserved).

MGUWr 856p/9/I, 1280p, 1280p/1, 1948p, 1959p, 2096 (counterpart of 1948p), 2218p, 2424p, 2471p, 2496p, 2504p, 2508p; KRAM-P 54/127/I, 54/280, 54/281, 54/282, 54/283/I & II, 54/284, 54/332/I, 54/338/I, 54/378, 54/381, 54/452 (counterpart of 54/456), 54/454, 54/455, 54/456, 54/747, 54/748, 54/749, 54/750 (several fragments), 54/907 (counterpart of 54/908), 54/908, 54/1117; MfN 1981/990; MZ VII/53/399.

Type locality. Sośnica near Wrocław, Lower Silesia, SW Poland.

Type stratum. Grey clay of the Flamy Clay Horizon in the upper part of the Poznań Formation.

Age. Pontian, Late Miocene (Dyjor et al. 1998).

Emended diagnosis. Fruit with two pairs of horns; fruit ca. 1.5 times wider than high, regularly obtriangular in outline, slightly truncate at the base, with a small, well-pronounced scar; neck without corolla, sunk into the upper surface of the fruit, not protruding beyond the line joining raised bases of the long upward pointing upper horns; fruit head relatively long and narrow; tubercles small; lower horns sturdy, located very close to the fruit base.

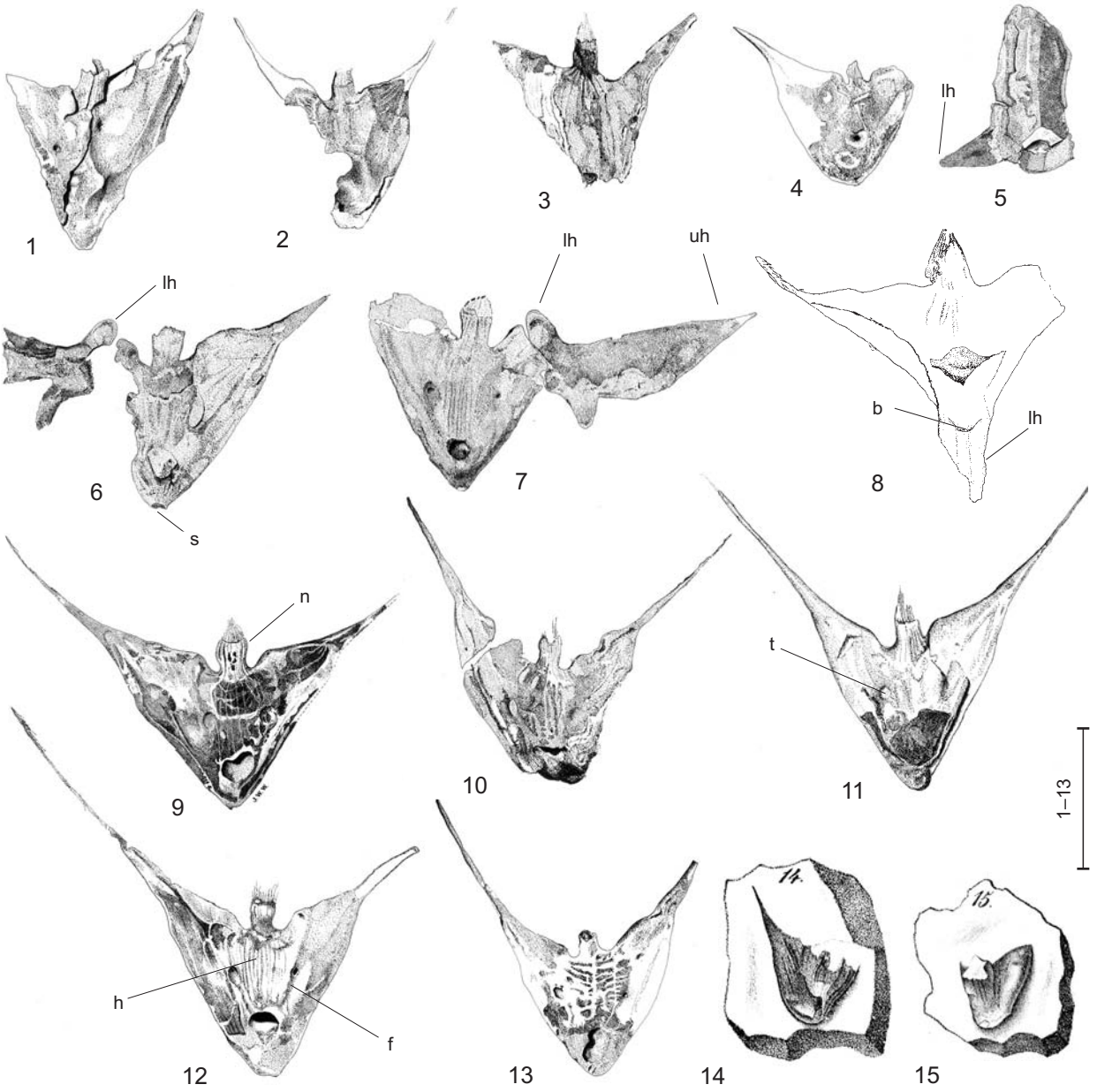


Fig. 1. *Trapa silesiaca* Goeppert emend. Wójcicki & Zastawniak; scale bar 1 cm. **1** – lectotype (MGUWr 812p), **2** – MGUWr 814p (syntype of *T. bifrons* Goepp.), **3** – MGUWr 1959p, **4** – MGUWr 656p/2 (syntype of *T. bifrons* Goepp.), **5** – KRAM-P 54/747, **6** – KRAM-P 54/452 (counterpart of KRAM-P 54/456), **7** – KRAM-P 54/456, **8** – MfN 1981/990, **9** – KRAM-P 54/908 (counterpart of KRAM-P 54/907), **10** – MGUWr 2424p, **11** – MGUWr 2504p, **12** – epitype (KRAM-P 286; specimen selected as neotype of *T. silesiaca* by Zastawniak et al. 1996), **13** – KRAM-P 54/1117, **14** – iconotype of *T. silesiaca* (Goeppert 1855: Pl. 25, fig. 14), **15** – iconotype of *T. bifrons* (Goeppert 1855: Pl. 25, fig. 15). **b** – base of lower horn, **f** – frame, **h** – head, **lh** – lower horn, **n** – neck, **s** – scar, **t** – tubercle, **uh** – upper horn

Description. Fruits 9–14 mm high (including neck), width of fruit at the level of the upper horns 14–26 mm; fruit about 1.3–1.6 times as wide as high; fruit head (3)5–8 mm long, its upper end located below the line joining the raised bases of the upper horns, bearing neck usually gradually broadening towards the base; neck 1.5–3.0 mm long and up to 2 mm broad, mostly not protruding beyond the line joining the bases of the upper horns; apical aperture with a ring of upward-pointing hairs; surface of fruit head and neck finely ribbed; upper horns narrowly triangular in outline, 6–11 mm long, characteristically slightly raised at base, gradually attenuate into straight elongate, thin, spine-like tips, ascending (30°–55°), with a smooth surface except for the at least 7–8 mm long, retrorsely barbed spines (harpoons); presence of mat areas excluded (in Latin *areolae impressae*

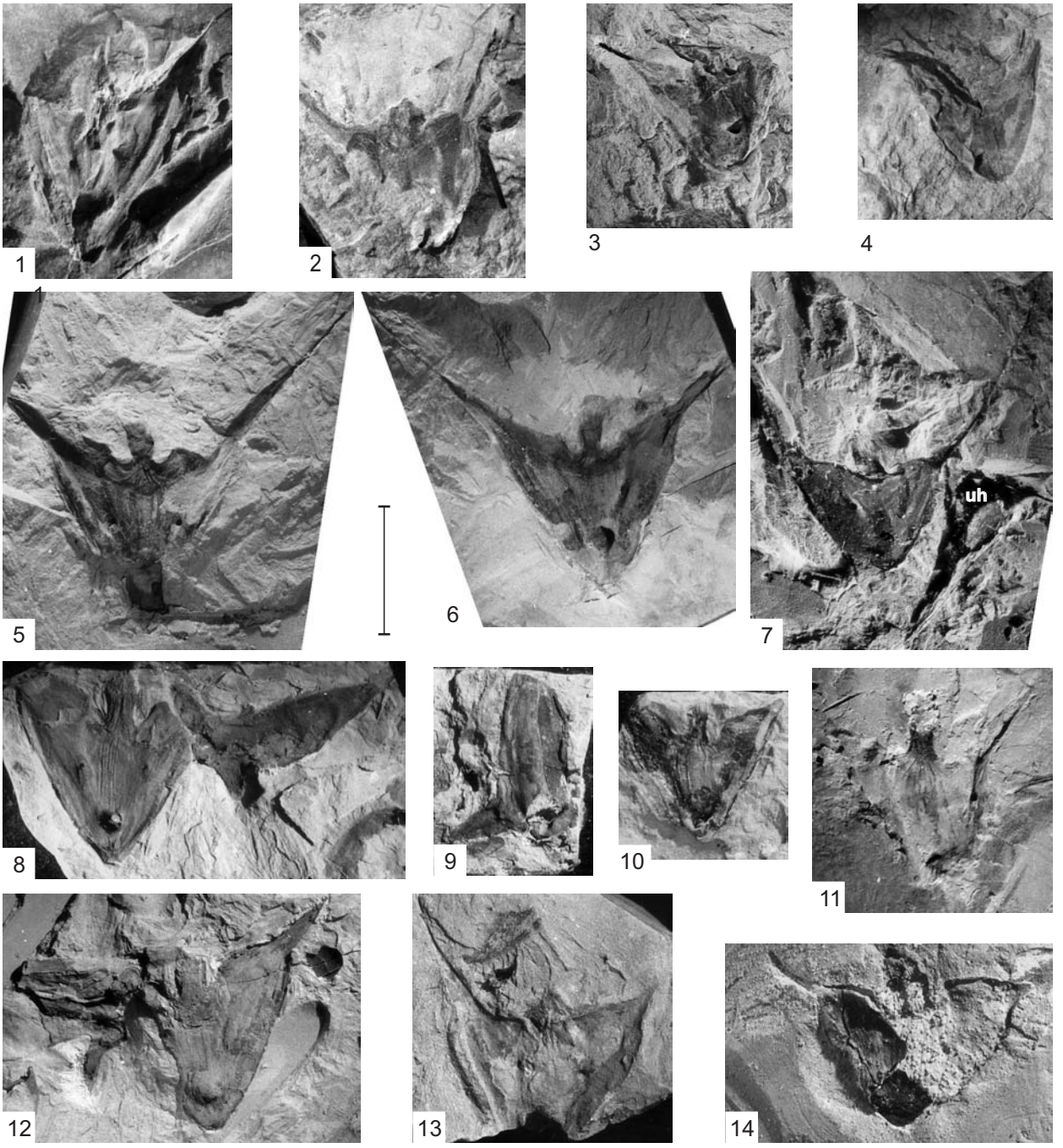
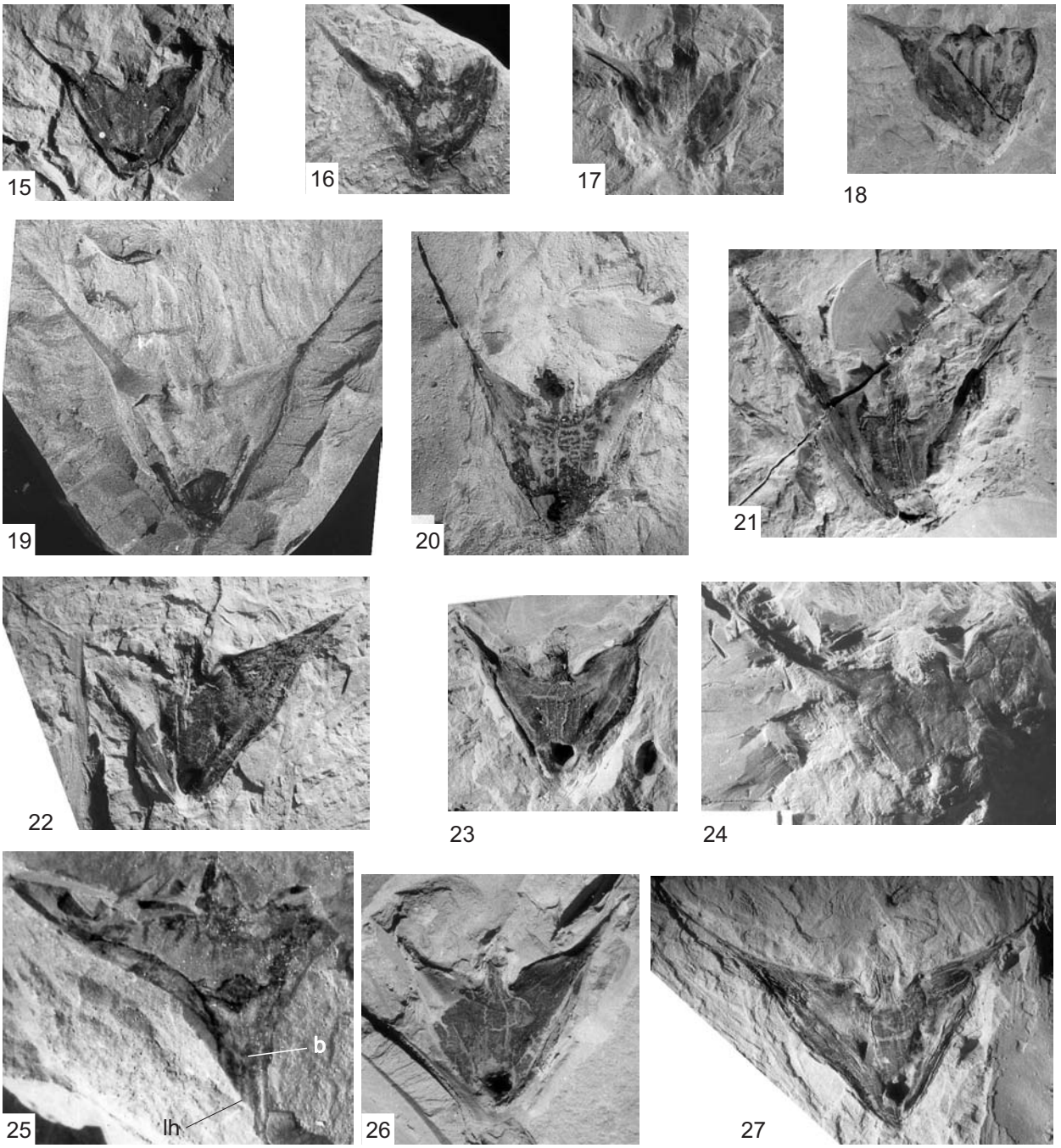


Fig. 2. *Trapa silesiaca* Goeppert emend. Wójcicki & Zastawniak; scale bar 1 cm. **1** – lectotype (= Fig. 1: 1; MGUWr 812p), **2** – MGUWr 814p (= Fig. 1: 2; syntype of *T. bifrons* Goepp.), **3** – MGUWr 656p/2 (= Fig. 1: 4; syntype of *T. bifrons* Goepp.), **4** – MGUWr 656p/1 (syntype of *T. bifrons* Goepp.), **5** & **6** – epitype (part and counterpart; KRAM-P 54/285 & 54/286 = Fig. 1: 12), **7** – KRAM-P 54/283/I & II, **8** – KRAM-P 54/456 (= Fig. 1: 7), **9** – KRAM-P 54/747 (= Fig. 1: 5), **10** – KRAM-P 54/748, **11** – MGUWr 1959p (= Fig. 1: 3), **12** – KRAM-P 54/452 (= Fig. 1: 6; counterpart of KRAM-P 54/456), **13** – MGUWr 2508p, **14** – KRAM-P 54/749, **15** – KRAM-P 54/280, **16** – MZ VII/53/399, **17** – MGUWr 1948p, **18** – MGUWr 2096p (counterpart of

– morphological structures present in some *Trapa* species at the base and/or adaxial part of the upper horns); lower horns slightly retrorse or horizontal, straight, not less than 6 mm long, inserted slightly asymmetrically in ca 2/5 from the fruit base or below; frame of fruit (in Latin *linea* [*costa*] *media* – protruding rib between upper and lower horns framing the fruit head) well-developed; small tubercles present on the fruit frame between the bases of the upper and lower horns; lower part of fruit body regularly obtriangular in outline, bearing, on one side of the surface, five protruding longitudinal ribs; fruit base with a small smooth ring, up to 1 mm high; basal scar less than 1 mm in diameter.



MGUWr 1948p), **19** – MGUWr 2504p (= Fig. 1: 11), **20** – KRAM-P 54/1117 (= Fig. 1: 13), **21** – MGUWr 2424p (= Fig. 1: 10), **22** – KRAM-P 54/907 (counterpart of KRAM-P 54/908), **23** – KRAM-P 54/282, **24** – KRAM-P 54/281, **25** – MfN 1981/990 (= Fig. 1: 8), **26** – KRAM-P 54/284, **27** – KRAM-P 54/908 (= Fig. 1: 9). **b** – base of lower horn, **lh** – lower horn, **uh** – fragment of fruit with upper horn

DISCUSSION

Goeppert (1855) gave only a very short Latin diagnosis (*T. nucibus bicornibus sulcatis integris, cornubus oppositis elongatis in spinam attenuatis*) and a schematic drawing for his new species, *Trapa silesiaca*. This lack of a precise characterization of the species resulted in doubts about its exact interpretation already expressed by Boulay (1890).

In 1906 Menzel slightly supplemented Goeppert's diagnosis of *T. silesiaca* but included into this species fossil fruits from another Late Miocene locality (Rauno = opencast mine Henkel near Senftenberg, Germany) representing an evidently different *Trapa*-morphospecies.

This caused further misinterpretations of the species (e.g. Kirchheimer 1937, 1957, Miki 1952). Recently Mai (2001) determined the fruits from Rauno as *Hemitrapa heissigii* Gregor following Gregor's (1982) sugestion that they partially represented this species. The problem of their classification is more complex and requires separate detailed studies.

For the purpose of providing a precise application of the name *T. silesiaca*, Zastawniak et al. (1996) selected the specimen (KRAM-P 54/286) from a new collections from Sośnica housed in the W. Szafer Institute of Botany, Polish Academy of Sciences, Kraków (cf. Figs 1: 12 & 2: 5) as a neotype. Because the syntypes of the species have been rediscovered in Goeppert's original collection from Sośnica, the neotype must be replaced by a lectotype (Art. 9.6 of ICBN; Greuter et al. 2000) as it has been done above. It is very probable that the type specimen illustrated by Goeppert (1855: Pl. 25, fig. 14; see also Fig. 2: 14) as *T. silesiaca* is lost, but the one designated here as the lectotype (MGUWr 812p; Figs 1: 1 & 2: 1) is most likely its counterpart.

Because the specimen selected as the lectotype is not well-preserved and does not reveal the diagnostic characters sufficiently clearly, the specimen KRAM-P 54/286 (and its counterpart KRAM-P 54/285) is designated here as an epitype for the purpose of providing a precise application of the name *T. silesiaca*, in accordance with Art. 9.7 of ICBN (Greuter et al. 2000).

Also, emendation and new circumscription of *T. silesiaca* has appeared necessary as the original diagnosis given by Goeppert (1855) is incomplete and incorrect. According to Goeppert, the fruit of *T. silesiaca* is characteristic in having only an upper pair of horns despite the appearance of a trace of lower horn being schematically marked on his drawing (Fig. 1: 14) and their being clearly visible on some of the syntype specimens. Misinterpretation of this structure arose probably due to the atypical position of the lower horns in *T. silesiaca* which are inserted very close to the fruit base. The same is true of the type specimens of *T. bifrons*, the second species described by Goeppert (1855) from Sośnica (cf. Fig. 1: 15), which, after the recovery of an almost complete set of upper horns from the sediment (probably Schlechtendal's label bearing such a statement is in the box with the original specimen) appeared to be conspecific with *T. silesiaca* (Figs 1: 2 & 2: 2; see also Menzel 1906, Meyer 1919). It is interesting that the variability of *T. silesiaca* fruits is rather small and restricted mostly to their size. Other slight differences in their morphology have probably been caused by fossilization and by the position of the fruit in the sediment, which makes interpretation difficult.

Three well-preserved fruit compressions/impressions along the plane of the lower horns [KRAM-P 54/452 & 456 (part and counterpart), KRAM-P 54/747 and MfN1981/990] clarify the problem concerning the presence of well-developed lower horns in this species (Fig. 1: 5, 6, 7, 8 and Fig. 2: 8, 9, 12, 25). It is then clear that *T. silesiaca* is a remarkably well-defined fossil species readily distinguished from the other known fossil and extant members of the genus (for references see Wójcicki et al. 1999, Kovar-Eder & Wójcicki 2001, Wójcicki & Wilde 2001, Wójcicki 2001) by its fruits ca. 1.5 times wider than high, regularly obtriangular in outline and slightly truncate at the base with a small but well-pronounced scar, a characteristic neck without the corolla, the neck sunk into the upper surface of the fruit and not protruding beyond the line joining characteristically raised bases of the long upward pointing upper horns. Additional diagnostic characters are a relatively long but narrow fruit head as well as small but well-developed tubercles on the fruit frame between the bases of the upper and lower horns, and sturdy lower horns located very close to the base of the fruit (Figs 1 & 2).

Trapa silesiaca Goepp. seems to have been relatively widely distributed in the Miocene of at least Central Europe, in contrast with some other Tertiary *Trapa* species known only from single or very few localities. This problem, however, is a subject of ongoing studies and will be presented separately. The revision of *T. silesiaca* from Sośnica presented in this paper is a necessary additional step towards understanding the patterns of speciation and evolutionary history of this complex genus.

REMARKS ON THE FOSSIL FLORA AND VEGETATION OF SOŚNICA

Among identified plant remains found in the fossil flora of Sośnica angiosperms predominated over gymnosperms and pterido-

phytes. The critical revision of this flora, which was started by Łańcucka-Środoniowa et al. in 1981, has resulted so far in studies of two families, Fagaceae (Walther & Zastawniak 1991) and Betulaceae (Zastawniak & Walther 1998). The list of taxa from that locality (Łańcucka-Środoniowa et al. 1981) has been recently supplemented by a new extinct genus *Limnobiophyllum* Krassilov emend. Z. Kvaček (Araceae) represented by *L. expansum* (Heer) Z. Kvaček. Detailed studies of megaspores of the water fern *Salvinia* have indicated that they are characteristic of the *S. intermedia* Dorofeev complex associated with *S. mildeana* Goeppert vegetative remains (Collinson et al. 2001). *Dombeyopsis lobata* Unger and *Smilax* sp. are new taxa for the flora of Sośnica recently determined by Z. Kvaček (pers. comm). In addition, presence of *Prunus padus* L. *fossilis* was confirmed (D.H. Mai pers. comm.) and cuticular analysis of a specimen determined as *Persea speciosa* Heer (Raniecka-Bobrowska & Czeczott 1958) indicated that its cuticle is characteristic of *Salix* (H. Walther pers. comm.) with the implication that the leaves of Lauraceae are not represented in that flora.

On the basis of the Sośnica fossil material (Tab. 1) the following main types of vegetation can be reconstructed. The area was dominated by a deciduous mixed forest with prevalence of broad-leaved trees and shrubs, of whose near relatives now grow in Europe, e.g. *Quercus, Acer, Fagus, Betula, Carpinus* and *Alnus*. The nature of the forest varied, depending on the moisture content of soil. Marshy sites were

Table 1. Growth forms of plant megafossils from Sośnica

Canopy (a)	Understorey (b)	Shrubs (c)	Herbs (d)
ARCTOTERTIARY TAXA			
Amentotaxus	*Aralia*	*Dichostylis*	*Azolla*
Cephalotaxus	Fabaceae p.p.	*Distylium*	*Batrachium*
Glyptostrobus	Hammamelidaceae	Fabaceae p.p.	*Boehmeria*
Pinus	*Liquidambar*	*Hydrangea*	*Callitriche*
Taxodium	Loranthaceae	*Myrica*	*Carex*
Acer	*Parrotia*	*Leitneria*	*Decodon*
Alnus	*Prunus*	*Paliurus*	*Dulichium*
Betula	*Salix*	*Phyllanthus*	*Hypericum*
Carpinus	*Vitis*		*Juncus*
Carya			*Limnobiophyllum*
Celtis			*Ludwigia*
Eucommia			*Lycopus*
Fagus			*Najas*
Ostrya			Poaceae
Palaeocarya			Polygonaceae
Platanus			*Polygonum*
Populus			*Pseudoeoeuryale*
Pterocarya			*Rumex*
Quercus			*Salvinia*
Ulmus			*Scirpus*
Zelkova			Solanaceae
			Sparganium
			Trapa
			Typha
21 (31%)	9 (13%)	8 (12%)	24 (36%)
PALEOTROPICAL TAXA			
Tetraclinis	*Ampelopsis*		
Dombeyopsis	*Smilax*		
Nyssa	*Symplocos*		
3 (4%)	3 (4%)	0	0

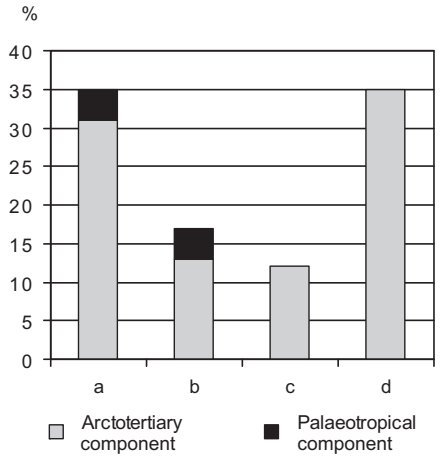


Fig. 3. Histogram of the percentual representation of diverse growth forms in the megafossil assemblage from Sośnica based on van der Burgh's (1994) method. **a** – canopy trees, **b** – understorey trees and lianas, **c** – shrubs, **d** – herbs

overgrown with a *Taxodium* forest with admixture of *Nyssa* and *Glyptostrobus* [its fossil wood was identified by Reyman (1956) as *Glyptostroboxylon*]. In moist places *Salix* and *Ulmus* dominated (their remains are most numerously represented in the assemblage), with various species of *Alnus*, *Carya*, *Liquidambar*, *Pterocarya*, *Platanus*, *Populus* and shrubby *Myrica* (Tab. 1). Less damp and probably at least slightly raised places were covered with a typical deciduous broad-leaved forest consisting mainly of *Fagus*, *Carpinus*, *Quercus*, *Parrotia* and *Zelkova*, shrubs of such genera as *Distylium*, *Hydrangea*, *Leitneria* and climbers represented by *Ampelopsis*, *Smilax* and *Vitis*. The presence of representatives of *Tetraclinis*, *Pinus*, *Paliurus* and Fabaceae suggests a relatively dryer environment. Margins of the forests and water bodies were overgrown with numerous herbaceous plants (e.g. *Carex*, *Decodon*, *Juncus*, Poaceae, *Polygonum*, *Rumex*). Relatively numerous plant remains of such genera as *Azolla*, *Batrachium*, *Callitriche*, *Dulichium*, *Limnobiophyllum*, *Ludwigia*, *Potamogeton*, *Pseudoeoeuryale*, *Salvinia*, *Scirpus*, *Sparganium*, *Trapa* and *Typha* clearly document the presence of well-developed, swamp, inshore and open water plant communities at Sośnica (see also Collinson et al. 2001).

The fossil flora of Sośnica is dominated by the arctotertiary element (Fig. 3), whereas the palaeotropical element is represented only by single specimens of a few taxa (*Ampelopsis*, *Dombeyopsis*, *Nyssa*, *Smilax*, *Symplocos* and *Tetraclinis*) as shown in Tab. 1. Such vegetation composition is characteristic of the so-called Cheylade "Florenkomplex" approximately 5.6 million years old (Mai 1995; see also Collinson et al. 2001). The domination of arctotertiary genera is typical of the Pontian within the area of the Northern Paratethys (Planderová et al. 1993).

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