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Sapindaceae (Aceroideae) from the late Miocene flora of Sośnica near Wrocław – a revision of Göppert's original materials and a study of more recent collections

HARALD WALTHER[1] and EWA ZASTAWNIAK[2]

[1] Staatliche Naturhistorische Sammlungen Dresden, Museum für Mineralogie und Geologie, Königsbrücker Landstraße 159, D-01109 Dresden, Germany; e-mail: h.walther.dresden. @t-online.de

[2] W. Szafer Institute of Botany, Polish Academy of Sciences, Lubicz 46, 31-512 Kraków, Poland; e-mail: e.zastaw@ib-pan.krakow.pl

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ABSTRACT. The results of a revision and new studies of macroscopic plant remains of *Acer* (Sapindaceae s.l., including Aceraceae) from the late Miocene (=Pannonian) flora of Sośnica near Wrocław are presented. The following leaf species of the genus *Acer* L. occur in this flora: *A.vindobonense* (Ettingshausen) Berger, *A. subcampestre* Göppert, *A. tricuspidatum* Bronn, *A. integrilobum* Weber sensu Walther, and *A. aegopodifolium* (Göppert) Bajkovskaja ex Iljinskaja. For three of the species an emended diagnosis is given. The leaf species have been described on the basis of morphological analysis; the epidermis was preserved and investigated only for *A. tricuspidatum* Bronn. These fossil leaf species are accompanied by the fruits of the fossil taxa *A. campestrianum* Dorofeev and *Acer* sp. div.

KEY WORDS: fossil leaves, fruits, *Acer*, revision, late Miocene, Poland

INTRODUCTION

The remains of *Acer* leaves and fruits, found in the Neogene and also in the late Palaeogene floras of Europe and Asia, have been the subject of numerous monographic studies (among others Pax 1885, 1902, Walther 1972, Procházka & Bůžek 1975, Tanai 1983, Wolfe & Tanai 1987, Ströbitzer-Hermann 2002). Fossil leaves of *Acer* are conspicuous, having mostly a characteristic shape and would seem to be easily identifiable. In addition, the discovery of fruit remains, also of diagnostic value, increases the chance of properly identifying their taxonomic affinity. The first palaeobotanist who described the leaves of Tertiary *Acer* species was Bronn (1837–1838) who illustrated two leaves of *Acer tricuspidatum* either from Salzhausen or Chomotau (Z. Kvaček, pers. comm.). Intention of this paper is to continue a series of taxonomical revision of the Sośnica flora.

PREVIOUS STUDIES ON THE ACER SPECIES FROM THE LATE MIOCENE OF SOŚNICA

Göppert (1852, 1855) distinguished seven *Acer* species on the basis of leaf remains. He named them: *Acer subcampestre, A. ribifolium, A. oeynhausianum, A. cytisifolium, A. hederaeforme, A. triangulilobum,* and *A. strictum*. He also illustrated three winged fruits of *Acer* naming them "Fructus *Aceris*" and one set of remains labelled "Semen *Aceris*". Most of the

specimens from Göppert's original collection have not been preserved.

Heer (1856) correctly identified the affinity of two leaves, which Göppert had described as *Platanus cuneifolia* (Göppert 1855, Pl. 12, figs 1, 3) as *Acer* leaves and assigned both to *Acer tricuspidatum* A. Br.

The first scientist to carry out a major critical revision of the determinations of *Acer* leaves from Sośnica was Pax (1885). He did this in a monograph of the genus *Acer* and repeated it in a comprehensive description of the Aceraceae (Pax 1902). In the Sośnica flora Pax found *Acer* remains representing two sections: *Palaeospicata* Pax and *Palaeocampestria* Pax. He assigned the leaf impressions of *Acer triangulilobum* Göpp. (Göppert 1855, pl. 23, fig. 6) to the former, while those of *Acer ribifolium* Göpp. (Göppert op. cit., Pl. 22, figs 18, 19) and one of the leaves identified by Göppert as *Platanus cuneifolia* Göpp. (Göppert op. cit., Pl. 12, fig.1) to the latter. Pax (1885) changed designations of the leaves of *Acer cytisifolium* Göpp., *A. hederaeforme* Göpp., and *A. oeynhausianum* Göpp., ascribing them to *Liquidambar europaeum miocenicum* (= *L. europaea* A. Br.); he also recognized *Acer strictum* Göpp. to be a leaf representing another genus, *Vitis teutonica* A. Br. which Knobloch (1969) designed to *V. stricta* (Göpp.) Knobloch.

In his revision of the flora of Sośnica, Meyer (1919) supported in part Pax's (1885) opinion that in Sośnica representatives of the section *Palaeocampestria* Pax occur, in the form of leaves and two fruits of *Acer subcampestre* Göpp., related to the recent species *A. campestre* L. (Göppert 1855, Pl. 24, figs 8, 9), and the leaves of another taxon, *Acer ribifolium* Göpp. In addition, Meyer (op. cit.) illustrated an impression of a maple winged fruit, applying to it the specific name of the leaf species – *Acer trilobatum* (Sternb.) A. Br.

MATERIAL AND METHODS

Among the original material from Göppert's collection, housed in the Institute of Geological Sciences, Wrocław University, only 3 specimens were found of the 15 fossil remains assigned by Göppert to the genus *Acer*. Additionally, three specimens of *Acer* leaves labelled *Platanus cuneifolia* and *P. guillelmae* and 2 specimens which Göppert had asigned to *Rhus (R. aegopodifolia* and *R. quercifolia*) have been preserved. To this small number of specimens new materials, collected after 1945, have been added (Łańcucka-Środoniowa et al. 1981); collectively they are in the possession of the Institute of Geological Sciences, Wrocław University (MGUWr), the W. Szafer Institute of Botany, Polish Academy of Sciences in Krakow (KRAM-P 54), the Museum of the Earth, Polish Academy of Sciences in Warsaw (MZ) and the Geological Museum of the State Geological Institute in Warsaw (IG). Fossil material was in general determined on the basis of morphological features of leaf and fruit remains, although in one case investigation of the anatomical structure (cuticular analysis) of the epidermis was succesfully conducted; the slide is housed in the Museum of Mineralogy and Geology, Dresden, Germany (MMG). On the other leaf impressions plant tissue is visible but it was impossible to obtain cuticular preparations from it.

The terminology used in the morphological description of the leaves follows that by Hickey (1973) and Ash et al. (1999).

DESCRIPTION OF TAXA

Family **SAPINDACEAE**
Subfamily **ACEROIDEAE**

Acer L.

Acer vindobonense (Ettingsh.) Berger

Fig. 1

1851 *Sterculia vindobonensis* Ettingshausen, p. 20, Pl. 4, fig. 2 (holotype – coll. No.: 1 1851/02/0021, Geologische Bundesanstalt, Vienna, Austria).

1867 *Acer sanctae crucis* Stur, p. 178, Pl. 5, Figs 9–12.

1906 *Acer polymorphum* Siebold & Zucc. *miocenicum* Menzel; Menzel, p. 100, Pl. 9, figs 7,8.

1920 *Acer polymorphum* Siebold & Zucc. *miocenicum* Menzel; Kräusel, p. 411, Pl. 6, fig.1.

1933 *Acer polymorphum* Siebold & Zucc. *miocenicum* Menzel; Menzel, Gothan & Sapper, p. 23, Pl. 5, fig. 8.

1955 cf. *Acer* (*Palmata*) *vindobonense* (Ettingsh.) Stur; Berger, p. 101, Text-fig. 140.

1955 *Acer* (*Palmata*) *sanctae-crucis* Stur; Berger, p.101, Text-figs 134–136.

1968 *Acer sanctae-crucis* Stur; Il'inskaya, p. 76, Pl. 4, figs 4, 5, Pl. 21, figs 4–6.

1972 *Acer sanctae-crucis* Stur; Walther, p. 49, Pl. 24, fig. 4, Pl. 38, Pl. 54, fig. 9.

1972 *Acer vindobonense* (Ettingsh.) Berger; Zastawniak, p. 45, Pl. 11, figs 5–7, Pl. 27, fig. 2.

1981 *Acer vindobonense* (Ettingsh.) Stur; Łańcucka-Środoniowa et al., Pl. 2, fig. 6.

1996 *Acer sanctae crucis* Stur; Zastawniak et al., p. 904, Pl. 301, fig. 5.).

2002 *Acer vindobonense* (Ettingsh.) Berger emend.; Ströbitzer-Hermann, p. 63, Pl. 7, figs 3–8.

For other synonyms see: Ströbitzer-Hermann (2002, pp. 63–65).

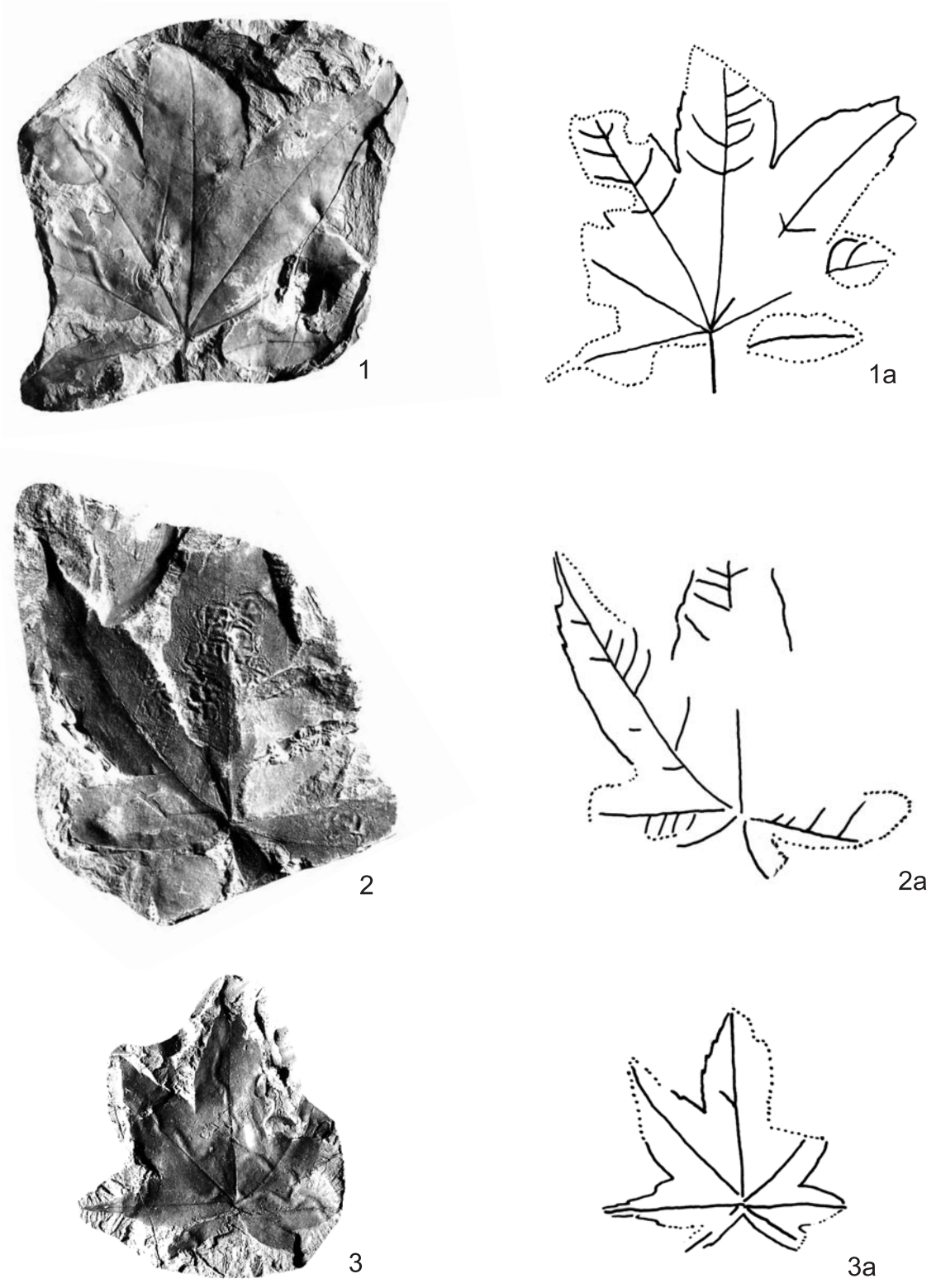


Fig. 1. *Acer vindobonense* (Ettingsh.) Berger. **1, 1a** – MZ VII/53/382; **2, 2a** – MGUWr 655p/2; **3, 3a** – MZ VII/53/403. Phot. A. Pachoński

Emended diagnosis. Leaves 5- or 7-palmately lobed, base cordate, lobes deeply incised, attenuate, acute, rarely acuminate, sinuses narrow and acute, leaf margin slightly simply or rarely double serrate.

Material. MGUWr 655p/2, MZ VII/53/382, MZ VII/53/403 and twin impression MZ VII/53/376; three leaf fragments and one twin impression.

Description. Leaves palmately 7-lobed, 4.3–5.5 cm long and about 3.4–5.5 cm wide. Base deep cordate, with petiole about 8 mm long. Central lobe and adjacent lateral lobes almost equal in size, elongate, oval or ovate. Apices of lobes acute or attenuate. Lobe margins, particularly in the upper part, with a few small teeth, arranged irregularly. Sinuses between the lobes acute and deep. Lowest lobes much smaller than the remaining ones, the next pair slightly smaller than the central lobe and the lateral lobes immediately below it. Apices of lobes acute. Venation actinodromous basal. The seven veins of the lobes end craspedodromously in their apices. Primary veins of the lowest lobes strongly abmedially curved. Delicate secondary veins branch off from the primary veins of the individual lobes at an angle of almost 90°, becoming faint towards the lobe apices. For further venation details see Walther (1972). Details of the anatomy of the epidermis are lacking.

Remarks. Section *Palmata* Pax is represented by leaves differing from all other *Acer* species always possessing more than 5 acutely tipped lobes which are crenulate-serrate or serrate (Pax 1885). The perpetual problem of the nomenclature of palmately 7-lobed, or rarely 5-lobed. Tertiary maple species has been discussed many times, however, without any satisfactory solution (Knobloch 1969, Walther 1972, Zastawniak 1972, Kovar-Eder 1988). There has been no uniformity of view about the diagnostic importance of such morphological features as the nature of the margins (presence or absence of teeth) of 7-lobed leaves (Berger 1955, Knobloch 1969, Walther 1972, Kovar-Eder 1988). As a result of thorough morphological studies of the preserved leaf fragment of *Sterculia vindobonensis* Ettingsh. (Ettingshausen 1851, Pl. 4, fig.1), which is the holotype of *Acer vindobonense* (Ettingsh.) Berger (Berger 1955, Knobloch 1969), Ströbitzer-Hermann (2002) reconsidered this holotype (No. 1851/02/0021, Geologische Bundesanstalt, Vienna) and completed its diagnosis in the following way: „Blätter palmat, fünf- oder siebenlappig, Basis cordat, Lappen meist tief eingeschnitten, attenuat, acut oder selten acuminat, an der Basis verjüngt, Buchten eng und spitz, Blattrand fast ganzrandig, einfach oder selten doppelt serrat“. She found indistinct teeth on the leaf margins of the holotype. Because the leaves are not “almost entire”, and Ströbitzer-Hermann’s (2002) paper has not yet been published, her supplementary diagnosis can not be used. The authors of the present paper propose to change the diagnosis emended by Ströbitzer-Hermann (op. cit.) as suggested above.

It should be added, however, that one would not be able to interpret this feature correctly in specimens with slightly folded lobe margins.

Among the leaf remains of *Acer vindobonense* (Ettingsh.) Berger known from the European Neogene, the epidermis structure has been ascertained only in specimens from Klettwitz (=Wilhelminensglück, Upper Lusatia, late Miocene), named as *Acer polymorphum* Siebold & Zucc. *miocenicum* Menzel (Menzel, Gothan & Sapper 1933) and *Acer sanctaecrucis* Stur. It was Walther (1972, Pl. 38, figs 1,2,4–6,8) who examined and described their abaxial and adaxial epidermis.

Leaf specimens from the Sośnica flora with 7 lobes and serrate margins correspond to *A. vindobonense* (Ettingsh.) Berger. Because of the lack of suitable fossil material, it was impossible to examine the epidermis structure in the leaves from Sośnica.

Göppert (1855) did not mention leaves of this type in the Sośnica flora.

The morphological features of the leaves of the fossil species and their epidermis are similar to those of the contemporary *Acer palmatum* Thunb. from Japan and Korean Peninsula, which grows also in the Mixed Mesophytic Forest sensu Wang (1961) of northern Chekiang and North Kwangsi (China), and in Taiwan in the upper part of the so-called Evergreen Broadleaved Forest (Walther 1972, 2004, Ströbitzer-Hermann 2002). *A. palmatum* Thunb. appear as shrub or small tree to 8 m high (Wang 1961).

Maples from sect. *Palmata* Pax occurred in central Europe from the late Miocene to the early Pliocene, as an ancillary element in zonal Tertiary mesophytic deciduous broadleaved forest (among others Walther 1972, Ströbitzer-Hermann & Kovar-Eder 2003).

Acer tricuspidatum Bronn

Figs 2–4

1823 *Phyllites lobatus* Sternberg, p. 37, Pl. 35, fig. 2.
1825 *Phyllites trilobatus* Sternberg, p. 42, Pl. 50, fig. 2.

1838 *Acer tricuspidatum* Bronn, p. 865, Pl. 35, figs 10a, b (holotype – missing).

1845 *Acer trilobatum* Al. Braun, p. 172.

1845 *Acer productum* Al. Braun, p. 172.

1847 *Acer productum* A. Br.; Unger, p. 131, Pl. 42, figs 1–9.

1847 *Acer vitifolium* A. Br.; Unger, p. 133, Pl. 43, fig. 10.

1851 *Acer patens* Al. Braun in Stizenberger, p. 84.

1851 *Acer bruckmannii* Al. Braun in Stizenberger, p. 84.

1855 *Acer tricuspidatum* A.Br.; Heer, p.14, Pl. 2, fig. 3.

1855 *Acer ribifolium*; Göppert, p. 34, Pl. 22, fig. 18 (non 19).

1855 *Platanus guillelmae*; Göppert, p. 21, Pl. 12, fig. 5 (MGUWr 768p/1).

1855 *Platanus cuneifolia*; Göppert, p. 22, Pl. 12, fig. 3 (MGUWr 768p/2).

1859 *Acer brachyphyllum* Heer, p. 56, Pl. 111, fig. 15, Pl. 117, figs 10–13,

1859 *Acer bruckmannii* A. Br.; Heer, p. 54, Pl. 116, figs 6–10.

1859 *Acer crassipes* Heer, p. 55, Pl. 117, figs 1, 2.

1859 *Acer triangulilobum* Göpp.; Heer, p. 198, Pl. 155, fig. 5.

1919 *Acer trilobatum* (Sternberg) A. Br.; Meyer, p. 169 pro parte, Pl. 14, fig. 24 (leaf, non Pl. 15, fig. 9 – fruit).

1920 *Acer trilobatum* (Sternberg) A. Br.; Kräusel, p. 412, Pl. 8, fig. 6, Pl. 15, fig. 2 (non fig. 1).

? 1920 Spec. indet. (cf. *Kalopanax, Oreopanax*); Kräusel, p. 426, Pl. 8, fig. 2.

1968 *Acer tricuspidatum* Bronn; Walther, p. 363, Pl. 2, fig. 1 (neotype).

1972 *Acer tricuspidatum* Bronn; Walther, p. 56, Pl. 18, figs 1–4, Pl. 50, fig. 1 – holotype, figs 2–6.

1975 *Acer tricuspidatum* Bronn sensu novo; Procházka & Bůžek, p. 24, Pl. 22–24, Text-figs 2, 3, 4d, 5, 13.

1983 *Acer tricuspidatum* Bronn sensu Procházka & Bůžek; Hummel, p. 70, Pl.43, figs. 1–6, Pl. 44, figs 1–3a, Pl. 45, figs 1–4, Pl. 46, figs 1–4, Pl. 47, figs 1–6, Pl. 48, figs 1–10, Pl. 49, figs 1, 2; Fig. 28: 1–22, Figs 29, 30.

1988 *Acer tricuspidatum* Bronn subsp. *lusaticum* Walther; Mai & Walther, p. 173.

2003 *Acer tricuspidatum* Bronn sensu Procházka & Bůžek; Worobiec, p. 44, Fig. 6: 5, 5a, Pl. 19, fig. 4, Pl. 20, fig. 6.

For other synonyms: see Walther (1972).

Material. MGUWr 768p/1, 803p, 954p, 1186p/II, 2201p, 2359p, 5131p, KRAM-P 54/514, 54/954, 54/620; ten leaf impressions.

Description. Leaves 3-lobed, about 2.7–7.0 cm long and 2.7–6.5 cm wide. Petiole to 1.8 cm long. Base cuneate to rounded or subcordate. Lobes triangular; central lobe distinctly longer and wider than the lateral ones. Apex of central lobe acute to acuminate. Apices of lateral lobes acute, very slightly rounded at the tip. Leaf margins irregularly serrate to fine-serrate. Teeth of uneven size, more or less acute. Venation actinodromous. Primary veins of lateral lobes under a large acute angle with the primary vein of central lobe. Lateral veins craspedodromous, alternate or opposite, departing from the primary veins at an acute angle and running slightly curved to the marginal teeth. Venation of higher order not preserved. Leaf blade tough. Smaller leaves ovate-lanceolate, 3.1–3.5 cm long and 1.1–2.2 cm wide. Central lobe longer than the lateral ones, which are truncate or rudimentary. Petiole 5 mm long.

The epidermis structure (cuticle remains) has been studied from one leaf (KRAM-P 54/514, MMG So 46/80). Cuticle thin, that of the adaxial epidermis not preserved, abaxial epidermis consisting of polygonal cells 10–20–32 µm across (Fig. 4), rarely papillate, with straight or sometimes curved anticlines. Stomata anomocytic, round to round-ovate, 16–20 µm wide, (12) 20–32 µm long. Solitary rounded hair bases 6–8–10 µm across, hairs unicellulate (Fig. 4: 4), 60–80 µm long, 5–8 µm wide at the base, apex acute.

Remarks. The morphology of the preserved leaf remains is entirely consistent with that of *Acer tricuspidatum* Bronn and the epidermis structure as well as, solitary hairs on the abaxial epidermis, which are unicellulate with bulbous thickened base, displays the characteristics of this morphospecies *A. tricuspidatum* Bronn is known mainly from sediments associated with fossil riverside forest (Kräusel & Weyland 1959, Walther 1972, Procházka & Bůžek 1975, Walther in Mai & Walther 1988, Ströbitzer-Hermann 2002).

Göppert (1855) named the Sośnica material of *Acer tricuspidatum* Bronn either as *Acer ribifolium* Göpp., or included to the genus *Platanus* as *P. cuneifolia* Göpp., and *P. guillelmae* Göpp.

Acer tricuspidatum Bronn is widely distributed in central Europe, known from various locations and facies, from the early Oligocene to the late Pliocene (among others Walther 1972, Procházka & Bůžek 1975, Ströbitzer-Hermann 2002). The taxon is highly variable

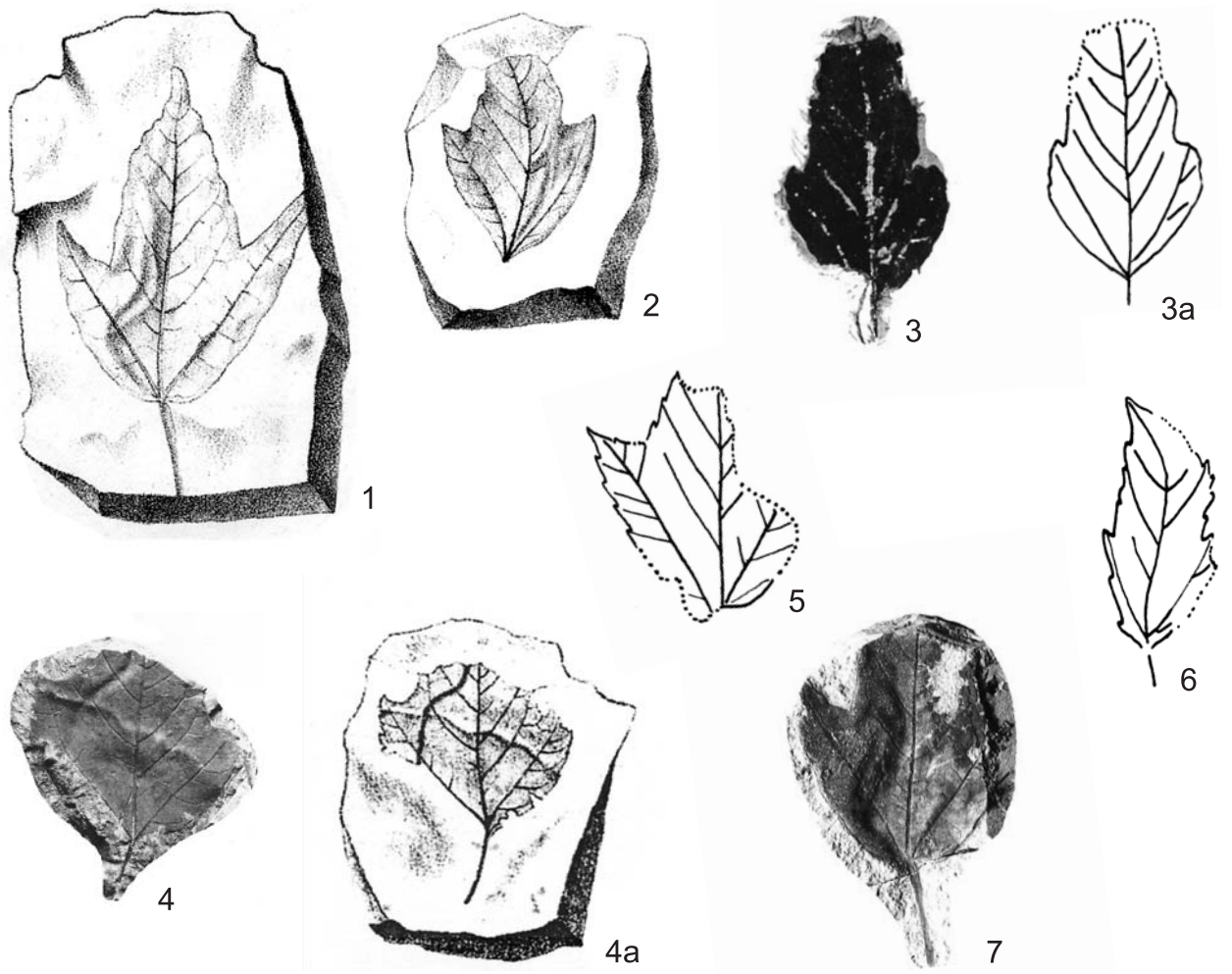


Fig. 2. *Acer tricuspidatum* Bronn. **1** – type of *Acer ribifolium* Göpp. (Göppert 1855, Pl. 22, fig. 18); **2** – type of *Platanus cuneifolia* Göpp. (Göppert 1855, Pl. 12, fig. 3); **3, 3a** – MGUWr 2359; **4** – type of *Platanus guillelmae* Göpp. (Göppert 1855, Pl. 12, fig. 5), **4a** – MGUWr 768p/1; – MGUWr 2359p; **5** – KRAM-P 54/620; **6** – MGUWr 2201p; **7** – MGUWr 803p. Phot. A. Pachoński

in leaf morphology. In view of this, Braun (1845) distinguished three morphospecies: *A. trilobatum*, *A. productum* and *A. tricuspidatum*, which were partly accepted by Heer (1859) who stressed, however, that they were connected by transitional forms and possibly represented one species. On the basis of statistical studies Hantke (1954, 1965) found that the supposed species were within the range of variability of one species, *Acer trilobatum* (= *A. tricuspidatum* Bronn; Walther 1968).

On the basis of detailed morphological, anatomical, statistical and biometric studies of *A. tricuspidatum* leaves from more than 13 localities (from the early Oligocene to the latest Miocene) Walther (1972) confirmed the wide range of variability among the leaves of this taxon. A stimulus to these studies was the acquisition of many leaf specimens in which it was possible to examine not only their morphological features but also the characteristic attributes of the epidermis structure, particularly that of the abaxial epidermis (Walther 1972).

The examinination of many forms of *A. tricuspidatum* leaves from the late Oligocene, through the Miocene to the end of the Neogene, revealed the appearance of leaves with a cuneate blade ("kesselförmigen Spreite") and irregularly fine-serrate margins. Walther (1972) did not conclude whether this was a genetically determined. Later on, Walther (Mai & Walther 1988) examined the cuticle of leaves of the same type from the Upper Pliocene of Thuringia (Berga) and found that – in spite of their slightly different morphology – they had the abaxial epidermis typical of *A. tricuspidatum* Bronn; in view of this he distinguished a new subspecies, *Acer tricuspidatum* Bronn ssp. *lusaticum* Walther.

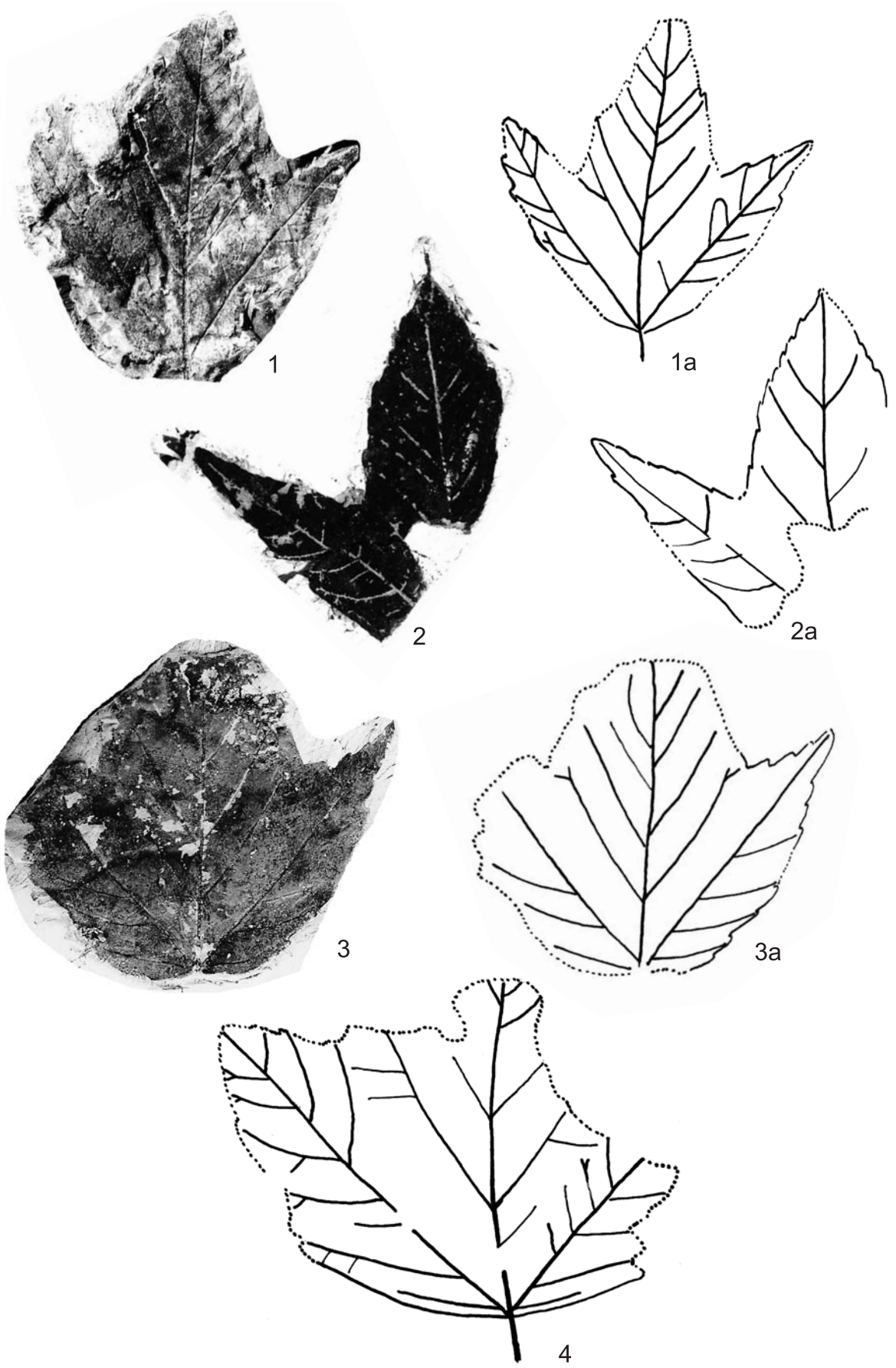


Fig. 3. *Acer tricuspidatum* Bronn. **1, 1a** – MGUWr 954p; **2, 2a** – MGUWr 1186p/II; **3, 3a** – KRAM-P 54/514; 4 – MGUWr 5131p. Phot. A. Pachoński

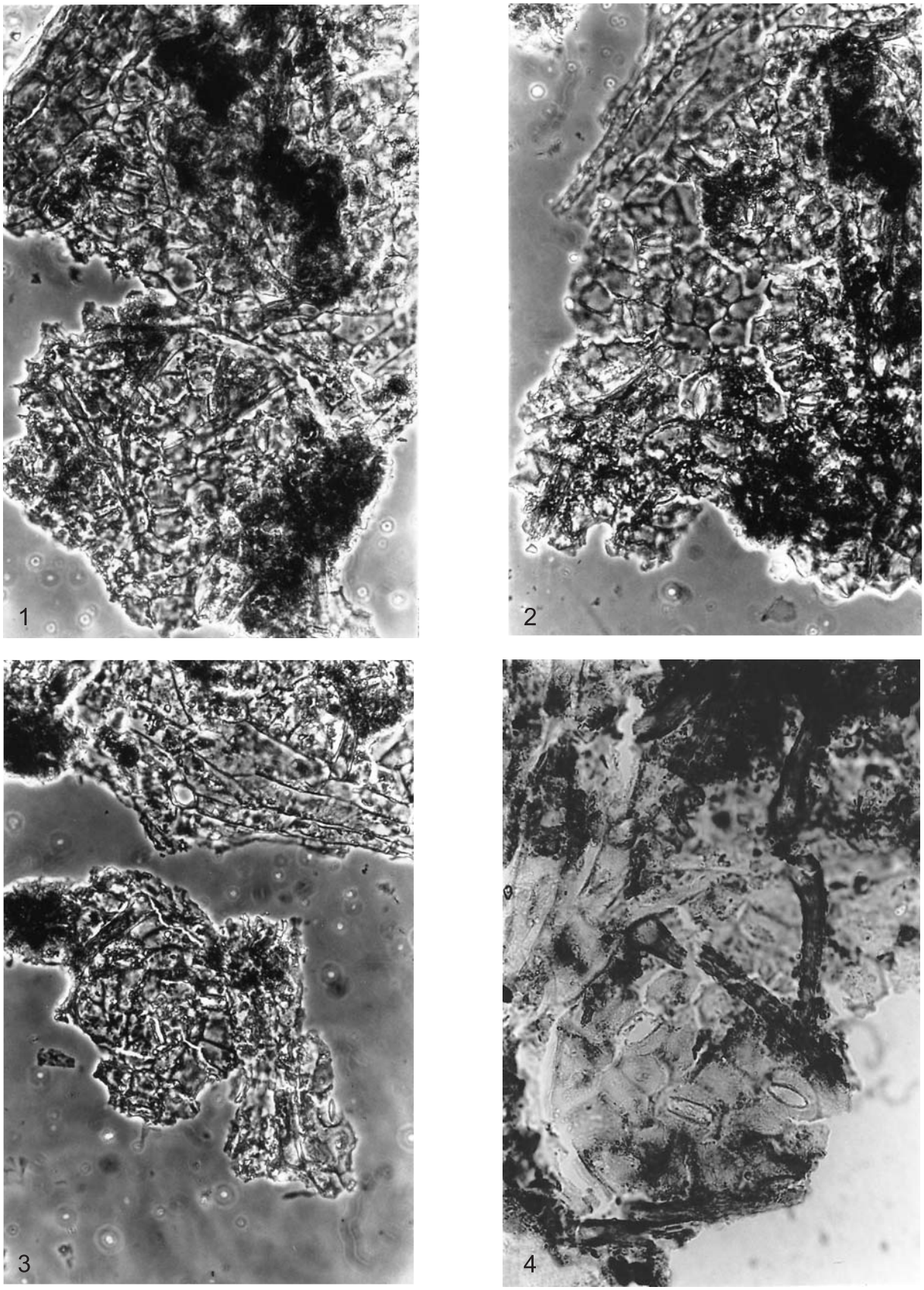


Fig. 4. *Acer tricuspidatum* Bronn, KRAM-P 54/514, slide MMG So 46/80. **1** – abaxial epidermis with trichome, ×400; **2** – abaxial epidermis ×400; **3** – abaxial epidermis, small veinlets with trichome base and unicellulate trichome, ×400; **4** – abaxial epidermis, stomata anomocytic, unicellulate trichome with bulbous base, ×650. Phot. H. Walther

Earlier, Procházka and Bůžek (1975) had distinguished, on the basis of the morphology of leaves, three forms within *Acer tricuspidatum*: f. *tricuspidatum,* f. *bruckmannii* and f. *productum*; however, they had not examined leaf anatomy, including the diagnostically important abaxial epidermis. This division was adopted in publications by Hummel (1983) and Worobiec (2003); in the former, in the Pliocene flora of Ruszów, the features of the leaf epidermis structure are characteristic of *A. tricuspidatum* Bronn; the leaves have almost exclusively a "cuneate" ("kesselförmige") base and fine-serrate margins. Ströbitzer-Hermann (2002) changed the status of *Acer tricuspidatum* Bronn ssp. *lusaticum* Walther reducing it to *Acer tricuspidatum* forma *pyrenaicum* (Rerolle) Ströbitzer-Hermann stat.nov. Ströbitzer-Hermann (Ströbitzer-Hermann 2002, Ströbitzer-Hermann & Kovar-Eder 2003) noticed morphological similarities between this form and the late Miocene *Acer pyrenaicum* Rerolle and *A. ilnicense* Iljinsk.

Despite a major effort by Ströbitzer-Hermann (2002) the palaeoecological and palaeoclimatic conditions apparently inducing for the occurrence of *A. tricuspidatum* forma *pyrenaicum* have not been unequivocally determined. It is, however, worth noting that this taxon was frequent in the Neogene floras of southern and south-western Europe, which could indicate its sclerophyllous character.

It is striking that the leaves of *A. tricuspidatum* Bronn forma *pyrenaicum* (Rerolle) Ströbitzer-Hermann stat. nov. with a cuneate base, characteristic of the floras of the late Miocene and Pliocene of Europe, are rare in the Sośnica flora. Specimens of *A. tricuspidatum* Bronn found in this flora represented the whole range of morphological variability, as in the case of e.g. the early Miocene flora of Břestany (Walther 1972). Therefore, all the maple leaves from the flora of Sośnica should be assigned to *A. tricuspidatum* Bronn though the details of their morphological and abaxial epidermis structure are limited to only one specimen.

Acer tricuspidatum Bronn is a typical element of swamp to mesophilous forests in the Tertiary floras of Europe and represents in the flora of Sośnica an element of azonal vegetation, alongside such species as *Quercus gigas* Göpp. emend. Walther & Zastawniak, *Quercus pseudocastanea* Göpp. emend. Walther & Zastawniak, and *Alnus gaudinii* (Heer) Knobloch & Kvaček (Walther & Zastawniak 1991, Zastawniak & Walther 1998).

Contemporary maple taxa from sect. *Rubra* Pax are considered as comparable with the fossil species (Heer 1859, Pax 1902, Hantke 1954, 1965, Berger 1955, Walther 1972). In Ströbitzer-Hermann's (2002) opinion, the contemporary *A. rubrum* L. is the nearest relative species (see also Walther 1972).

Acer subcampestre Göppert

Figs 5, 6

1855 *Acer subcampestre*; Göppert, p. 34, Pl. 22, fig. 16 ?, 17 (missing).
1861 *Acer subcampestre* Göpp.; Ludwig, p. 178, Pl. 69, fig. 3.
1906 *Acer subcampestre* Göpp; Menzel, p. 103, Pl. 6, figs 2, 10, 11.
1954 *Acer subcampestre* Göpp; Pimenova, p. 84, Pl. 26, figs 1, 2, 4, 5; fig. 3 – fruit.
1955 *Acer subcampestre* Göpp ; Yakubovskaya, p. 79, Pl. 7, figs 2, 3, 5.
1957 *Acer subcampestre* Göpp; Givulescu, p. 73, Pl. 12, fig. 1.
1961 *Acer subcampestre* Göpp; Il'inskaya & Shvaryova, p. 146, Pl. 2, figs 3–5, Pl. 4, figs 4–6.
1965 *Acer subcampestre* Göpp.; Kryshtofovich & Baykovskaya, p. 101, Pl. 26, fig. 5, Pl. 27, fig. 4, Pl. 28, figs 1–11.
1968 *Acer subcampestre* Göpp; Il'inskaya, p. 76, Pl. 4, fig. 6, Pl. 10, fig. 3, Pl. 11, fig. 6, Pl. 15, fig. 11, Pl. 25, figs 4–6, Pl. 51, fig.7.
1969 *Acer subcampestre* Göpp.; Givulescu & Ghiurca, p. 51, Pl. 16, figs 1, 3.
1974 *Acer subcampestre* Göpp; Shtephyrtza, p. 115, Pl. 8, fig. 5, Pl. 23, fig. 3.
1983 *Acer subcampestre* Göpp; Shvaryova, p. 130, Pl. 14, figs 7–10, Pl. 20, fig. 5, Pl. 36, figs 3, 4, Pl. 37, figs 1–3, Pl. 38, figs 1, 2, Pl. 41, fig. 3, Pl. 46, figs 7, 8, Pl. 49, fig. 6, Pl. 79, fig. 3; Fig. 31: 1–8, Fig. 32: 1–6.
1989 *Acer subcampestre* Göpp; Shvaryova, p. 70, Pl. 14, fig. 1, Pl. 28, fig. 4.
2003 *Acer subcampestre* Göpp; Shvaryova & Mamchur, p. 113, Pl. 20, fig.8, Pl. 69, fig.4.

Neotype designated here. Specimen MZ VII/53/75, fig. 5: 3. (counterpart MZ VII/53/74, fig. 5: 3a).

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

Type stratum. Flamy Clays Member, upper part of the Poznań Formation.

Age. Upper Miocene, Pannonian.

Emended diagnosis. Leaf palmately 5-lobed, wider than long, base subcordate,

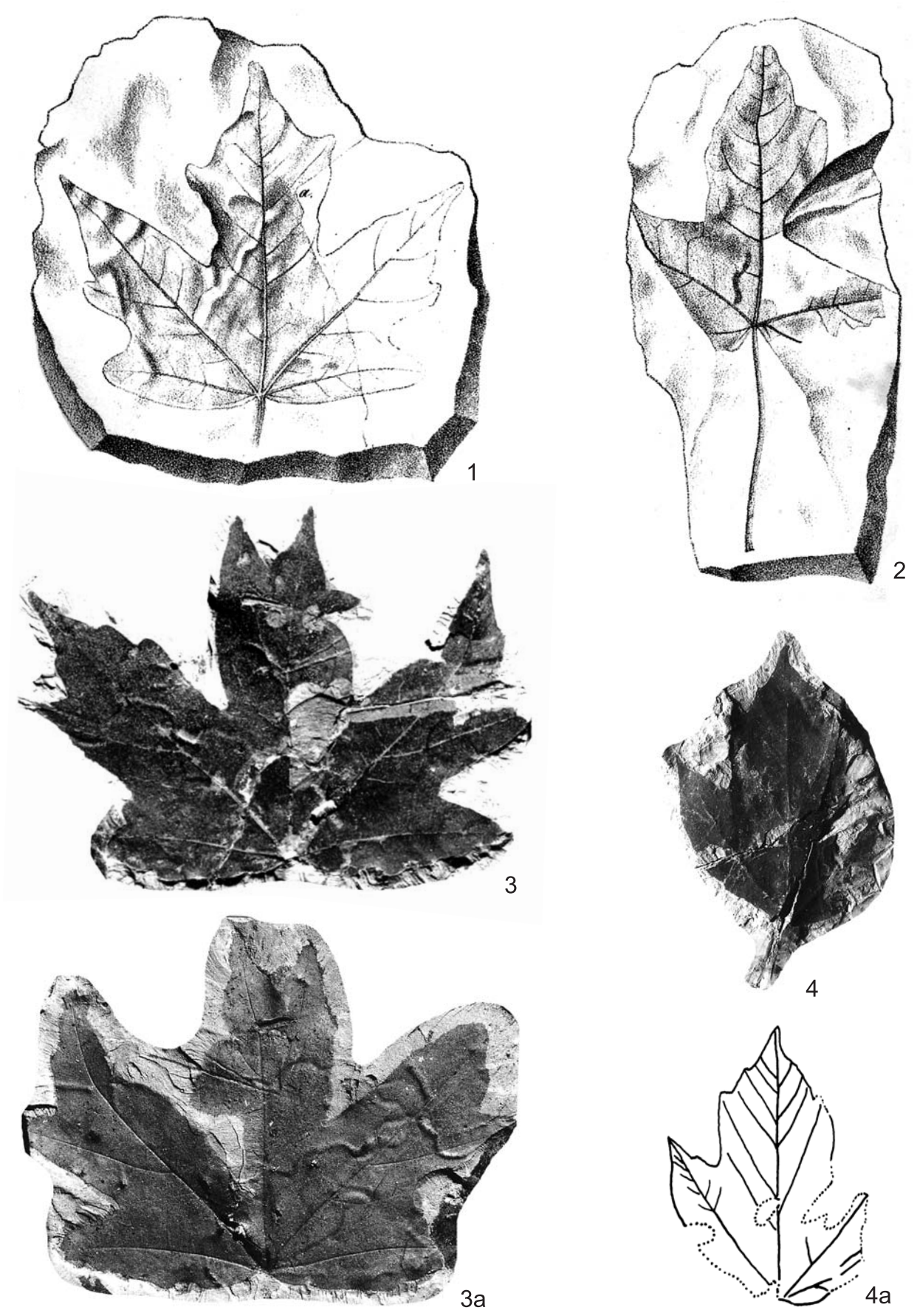


Fig. 5. *Acer subcampestre* Göpp. **1** – Göppert 1855, Pl. 22, fig. 17; **2** – Göppert 1855, Pl. 22, fig.16; **3** – neotype, MZ VII/53/75; **3a** – twin impression of the neotype – MZ VII/53/74; **4**, **4a** – KRAM-P 54/295. Phot. A. Pachoński

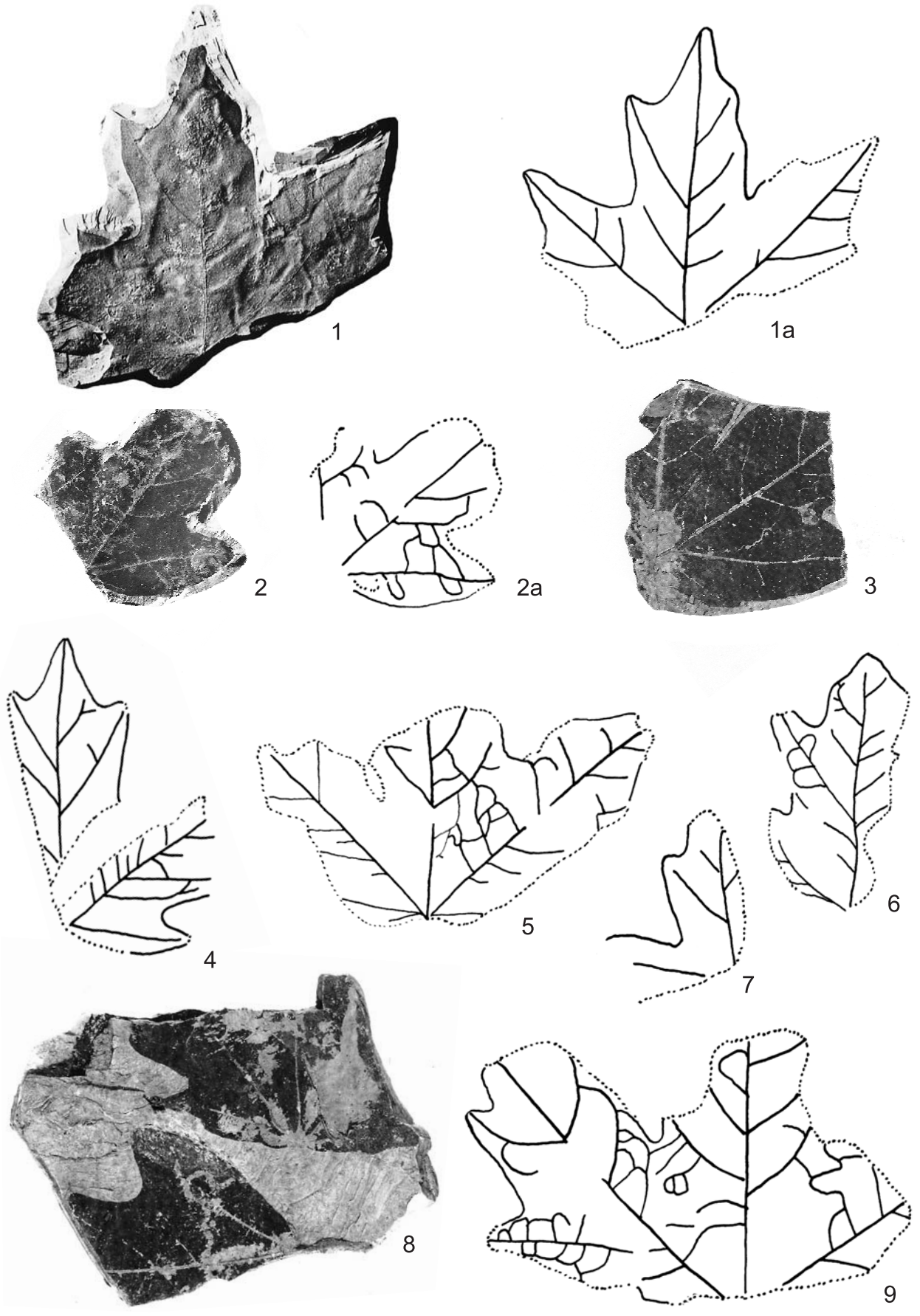


Fig. 6. *Acer subcampestre* Göpp. **1**, **1a** – KRAM-P 54/466; **2**, **2a** – MGUWr 2365p, **3** – IG 46.III.278; **4** – MZ VII/53/155; **5** – IG 46.III.280; **6** – MGUWr 1092p/1/III; **7** – MGUWr 1084p/2/II; **8** – IG 46.III.292; **9** – MGUWr 801p. Phot. A. Pachoński

terminal and lateral lobes nearly the same size, basal lobes smaller; lobe apices triangular, acute, terminal with two characteristic teeth, lateral ones with one abaxial tooth, basal with entire margins. Primary veins straight, reaching the apices of the lobes, secondary veins craspedodromous, terminating in the main teeth, secondaries of the basal lobes camptodromous.

Material. MGUWr 804p, 1084p/2/II, 1092p/1/III, 2365p, KRAM-P 54/295, 301 (twin impressions), 54/466/I, MZ VII/53/74, 75 (twin impressions), VII/53/155,VII/53/ 280, VII/53/292/I, II, IG 46.III.278, 46.III.280, 46.III.292/I, II; sixteen leaf impressions, two with twin impressions.

Description. Leaves palmately 5-lobed, 6.5 cm long and 8.7 cm wide. Base slightly cordate. Terminal lobe and adjacent lateral lobes almost equal in size, lowest lobes smaller. Lobe apices acute. Terminal lobe with two large rounded teeth, one on each side. Lateral lobes with one tooth on the abaxial side. Basal lobes with an entire margin. Angles between lobes acute. The primary veins run straight to the apices of the lobes, secondary veins craspedodromous, running directly to the teeth. Secondary veins in the lateral lobes camptodromous, anastomosing at the leaf margin. The characteristics of the anatomy of the epidermis are unknown.

Remarks. The species *Acer subcampestre* Göpp., sect. *Platanoidea* Pax, series *Campestria* (Pax) Pojarkova, was described by Göppert (1855) from the Upper Miocene of Sośnica. No original specimens of this species, illustrated in Göppert's publication (Göppert, op. cit., Pl. 22, figs 16, 17) were found, making it necessary to determine a neotype from new collections.

Leaves of this species are characterized by conspicuous large teeth on the terminal and the two upper lateral lobes. The characteristics of the anatomy of the epidermis in this fossil species have not been studied as yet.

Acer subcampestre Göpp. is reported from numerous Neogene localities, particularly in eastern Europe where it is known from the middle Miocene of the Ukraine (Pimenova 1954, Kryshtofovich & Baykovskaya 1965, Shvaryova 1989), Moldova (Yakubovskaya 1955, Shtephyrtza 1974), the Forecarpathians (Shvaryova 1983) and from the Pliocene of the Transcarpathians (Il'inskaya 1968, Shvaryova & Mamchur 2003) and Romania (Givulescu 1957, Givulescu & Ghiurca 1969).

According to Ströbitzer-Hermann (2002), it is probable that *Acer obtusifolium* Unger (Unger 1847, Pl. 43, fig.12) could be synonymous with *A. subcampestre* Göpp. because of their morphological similarity. In her opinion, *Acer subcampestre* Göpp. (including *A. obtusifolium* and *A. jurenakyi*) should be provisionally treated as a fossil species complex, which occurred in Europe from the middle Miocene to the end of the Plio-Pleistocene, mainly in the late Miocene, where it grew in humid mesophytic forest habitats, but it could also have occurred in azonal communities.

There are undoubtedly more maple species from the late Neogene floras described by different authors, such as e.g. *A. pseudocampestre* Unger, *A. divaricatum* Andreánszky, *A. jurenakyi* Stur, or *A. palaeosaccharinum* Stur (see e.g. Ströbitzer-Hermann 2002), which could belong to *A. subcampestre* Göpp. Until the epidermis structure of these fossil species and the range of their morphological variability are known, this must remain an open question.

Uncertain also are the relations between *A. subcampestre* Göpp. and contemporary species. Most often mentioned is the contemporary *A. campestre* L., whose area covers almost the whole of Europe, North Africa and northern Iran, and which is characterized by great morphological variability (see: Pax 1902, Oterdoom 1994). The association of *Acer miyabei* Maximowicz ssp. *miyabei* (Ströbitzer-Hermann 2002) with the fossil taxon can be settled only after further comparative studies of both the morphology and anatomy of the leaves.

In the flora of Sośnica – a typical locality for *A. subcampestre* Göpp. – this species is a thermophilous accesory element in mesophilous broad-leaved deciduous forest.

Acer integrilobum Weber sensu Walther

Fig. 7

1852 *Acer integrilobum*; Weber, p. 82, Pl. 22, fig. 5a, b.

1855 *Platanus cuneifolia*; Göppert, p. 22, Pl. 12, fig. 1 (MGUWr 765p).

1907 *Acer ribifolium* Göpp.; Pax, p. 55.

1919 *Acer ribifolium* Göpp.; Meyer, p. 170, Pl. 15, fig. 12 (MGUwr 765p).

1969 *Acer decipiens* Heer; Givulescu & Ghiurca, p. 51, Pl. 14, fig. 6, Pl. 17, fig. 33a, b, c.

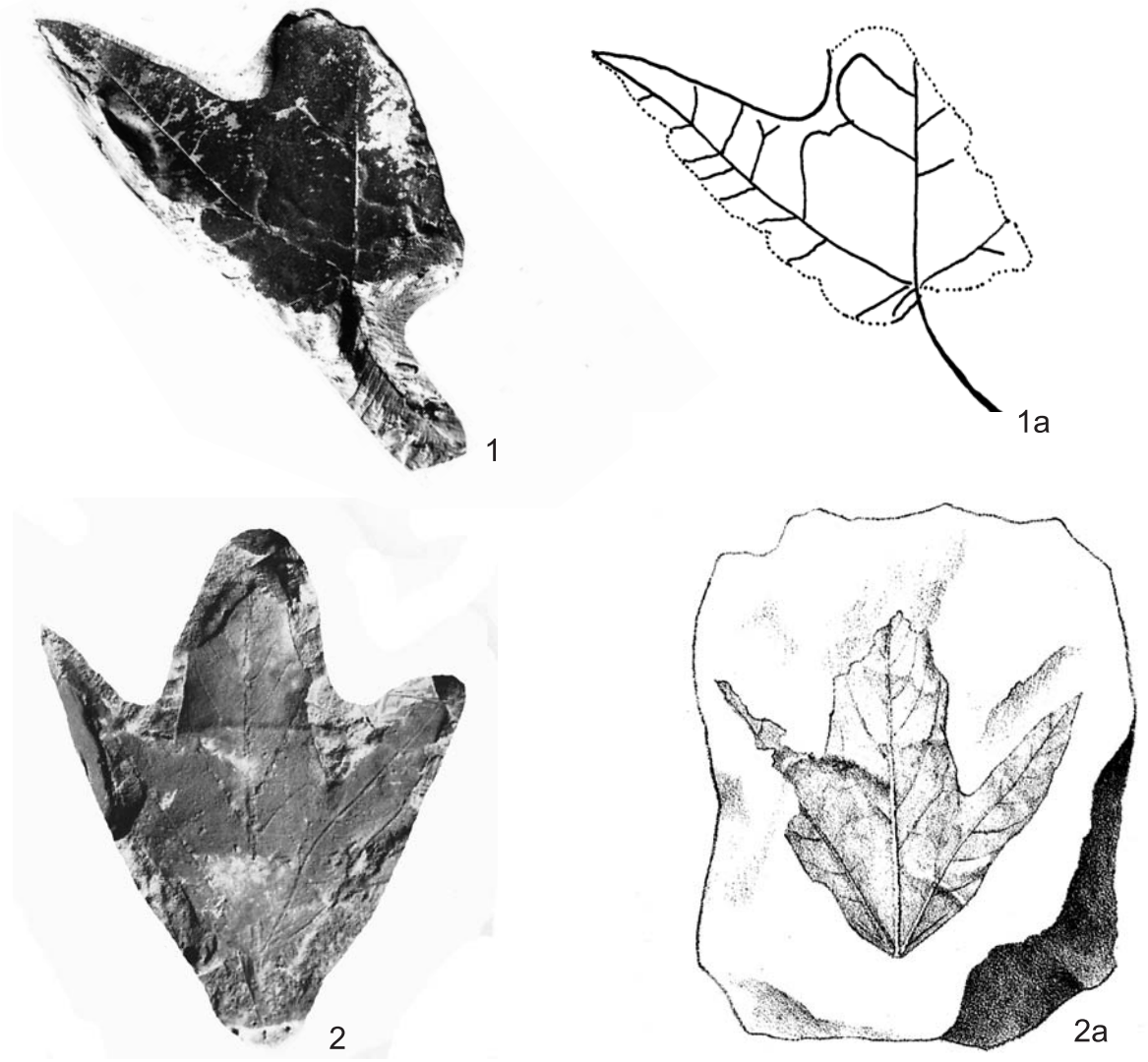


Fig. 7. *Acer integrilobum* Weber sensu Walther. **1, 1a** – MGUWr 5183p, **2** – MGUWr 765p **2a** – as *Platanus cuneifolia* Göpp. (Göppert 1855, Pl. 12, fig. 1). Phot. A. Pachoński

1972 *Acer integrilobum* Weber sensu Walther; Walther, p. 111, Pls 25, 26, 55.
1988 *Acer integrilobum* Weber; Kovar-Eder, p. 50, Pl. 6, fig 17, Pl. 11, figs 9–11.
1990 *Acer integrilobum* Weber; Givulescu, p. 125, Pl. 11, fig. 5, Pl. 37, fig. 5.
2003 *Acer integrilobum* Weber; Shvaryova & Mamchur, p. 113, Pl. 20, fig. 2, Pl. 78, figs 2–4.

M a t e r i a l. MGUWr 765p, 5183p; two leaf impressions.

D e s c r i p t i o n. Leaves 3-lobed, up to about 5.5 cm long, petiolate. Petiole to 2.4 cm long. Terminal lobe longer and wider than the acuminate lateral lobes. Leaf base cuneate to rounded with entire margin. Terminal lobe with a pair of unequal teeth. Midveins straight or slightly arched, running to the apices of the lobes. Secondary venation craspedodromous to semicraspedodromous. Anatomical features of the epidermis unknown.

R e m a r k s. Leaves of this type were referred by Göppert (1855) to the genus *Platanus*; later on Meyer (1919) identified them as maple leaves, including them into the species described from Sośnica as *Acer ribifolium* Göpp. from the section *Palaeocampestria* Pax. However, Meyer (op.cit.) erroneously identified a specimen photographed in his account (Meyer 1919, Pl. 15, fig. 12) with the illustration of *Acer ribifolium* Göpp. in Göppert's publication (Göppert 1855, Pl. 22, fig. 18). Göppert's specimen has been lost from the collection; however, the drawing of its leaf clearly shows that its margins are not entire, enabling one to identify it as a leaf of *Acer tricuspidatum* Bronn. On the other hand, the

leaf from Meyer's publication (Meyer, op. cit., Pl. 15, fig. 12) is a photograph of a specimen of *Platanus cuneifolia* (Göppert 1855, Pl. 12, fig. 1, MGUWr No 765p), i.e. *Acer integrilobum* Weber sensu Walther, a species whose leaf lobes have an entire margin.

According to Pax (1885), *Acer ribifolium* Göpp. would be an ancestral species of *A. monspessulanum* L. and *A. campestre* L., which separated in the Miocene. For 3-lobed *Acer* leaves with an almost entire margin, one should, however, use the earliest name, *Acer integrilobum* Weber. Pax (1902) mentioned this fossil species along with others in section *Palaeocampestria* Pax, erroneously quoting the species name as „*integrifolium*".

The oldest known locality of *Acer integrilobum* Weber sensu Walther is the early Oligocene flora of Bechlejovice in the northern Czech Republic (Kvaček & Walther 2004). It sporadically occurs in the Palaeogene volcanic floras (sensu Kvaček & Walther 2001, Walther 2004), such as the early Oligocene floras of Hammerunterwiesenthal (Walther 1998) and Kundratice (Kvaček & Walther 1998), the Upper Oligocene of Enspel (Köhler 1998), as well as in the marine sediments of the Central Paratethys in the area of Linz (Upper Oligocene, Kovar 1982). During the Neogene (Miocene to early Pliocene) the range of this fossil species expanded, covering southern and south-western Europe (e.g. Ströbitzer-Hermann 2002).

Of contemporary species, it is *Acer cappadocicum* Gleditsch (sect. *Platanoidea* Pax) and its varieties (see Krüssmann 1976) that are morphologically most similar to the fossil species. *A. cappadocicum* grows today in mountain forests of the Caucasus, Asia Minor to the Himalayas and the province of Yunnan in China, and occurs up to 3100 m a.s.l. However, the structure of the abaxial epidermis in the leaves of the contemporary species is completely different from that in *A. integrilobum*. In Ströbitzer-Hermann's opinion (Ströbitzer-Hermann 2002), the epidermis of another contemporary species – *A. campbellii* ssp. *wilsonii* (Rehder) de Jong from sect. *Palmata* Pax, series *Sinensis* Pojarkova – has certain features in common with that of *A. integrilobum*. As far as is currently known, no contemporary maple species can be associated with the fossil morphospecies *A. integrilobum*.

Acer aegopodifolium (Göppert) Bajkovskaja ex Iljinskaja

Figs 8–10

1855 *Rhus aegopodifola*; Göppert, p. 37, Pl. 25, fig. 10 (holotype – missing).

1855 *Rhus quercifolia*; Göppert, p. 37, Pl. 25, figs 6–9.

1919 *Rhus quercifolia* Göpp.; Meyer, p. 171, Text-fig. 18, Pl. 15, fig. 8, Pl. 16, fig. 17, Pl. 17 fig. 1.

1920 *Rhus quercifolia* Göpp.; Kräusel, p. 410, Pl. 14, figs 1, 2.

1951 *Rhus* cf. *diversiloba* T. & G.; Czeczott, Pl. 9, figs 19, 20.

1965 *Acer aegopodifolium* (Göpp.) Bajkovskaja; Shvaryova, p. 953.

1968 *Acer aegopodifolium* (Göpp.) Bajkovskaja; Il'inskaya, p. 67, Pl. 9, figs 12–15, Pl. 20, figs 4, 5.

1971 LX; Ferguson, p. 236, Fig. 43, A, B, Pl. 44 D.

1974 *Acer aegopodifolium* (Göpp.) Bajkovskaja; Zhilin, p. 57, Fig. 30.

1980 *Monopleurophyllum quercifolium* (Göpp.) Kotlaba; Zastawniak, p. 79, Fig.13: 1, 2.

1988 *Acer quercifolium* (Göpp.) Kovar-Eder comb.nov.; Kovar-Eder, p.51, Pl. 6, figs 14–16.

1999 *Acer aegopodifolium* (Göpp.) Bajkovskaja ex Iljinskaja; Schmitt & Kvaček, p. 84, Pl. 1, figs 1–4, Text-fig. 3.

Neotype designed here. Specimen MGUWr 1559p/1, Fig. 9: 10.

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

Type stratum. Flamy Clays Member, upper part of the Poznań Formation.

Age. Upper Miocene, Pannonian.

Emended diagnosis. Leaves trifoliolate. Apical leaflet largest, symmetrical, with cuneate base and acuminate apex, and teeth on both sides. Lateral leaflets asymmetrical, cuneate-rounded at the base, apex acuminate. A large lobe is present at the base of the outer margin of each lateral leaflet. Venation craspedodromous-camptodromous.

Material. MGUWr 539p/1/II, 554p, 655p/1, 664p/3, 962p/2, 962p/3/II, 978p/4, 1011p/17, 1015p/14/I, 1559p/1, 1559p/2, 1559p/3, 1559p/4, 1559p/5, 1910p/II, 2037p, 2051p, 2283p/I, 2315p/II, 2364p, 2369p, KRAM-P 54/298, 54/299, 54/557, 54/976, MZ VII/53/235, IG 46.III.128, 46.III.129, 46.III.219; nine impressions of several joined leaflets and twenty impressions of individual leaflets.

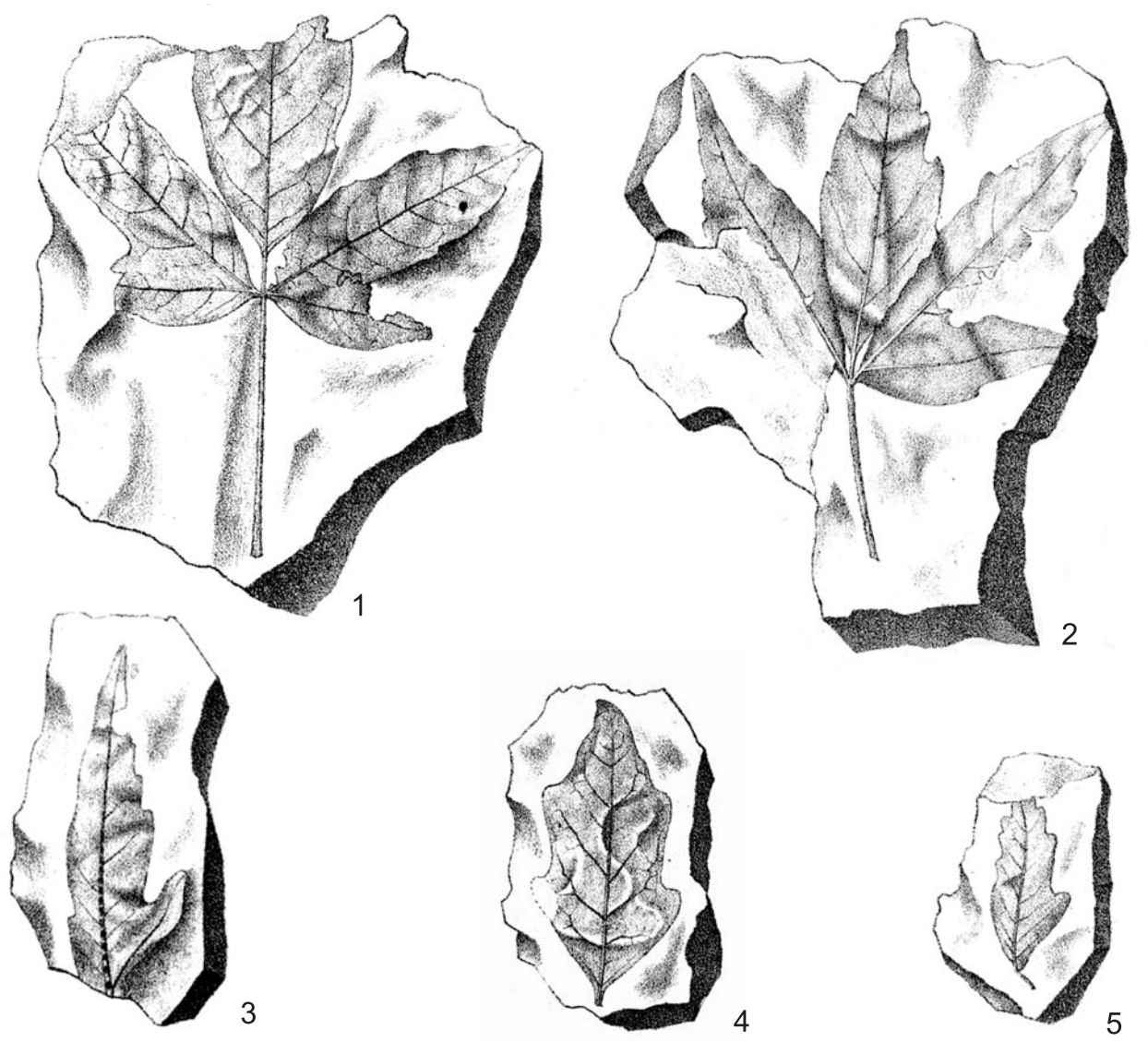


Fig. 8. *Acer aegopodifolium* (Göpp.) Bajkovskaja ex Iljinskaja. (*Rhus quercifolia* Göpp.). **1** – Göppert (1855), Pl. 25, fig. 6; **2** – ibidem, Pl. 25, fig. 10; **3** – ibidem, Pl. 25, fig. 8; **4** – ibidem, Pl. 25, fig. 9; **5** – ibidem, Pl. 25, fig. 7

D e s c r i p t i o n. Leaves with long petioles, palmate, composed of three leaflets of different size, 3.0–6.0 cm long and 1.0–3.0 cm wide. Apical leaflet largest, symmetrical, with cuneate base and acuminate apex, with small and large teeth on both margins. Lateral leaflets asymmetrical, cuneate-rounded at base, apex acuminate. At the base of the outer margin of the lateral leaflets a large lobe is usually present. Outer margins of lateral leaflets variable, lobed, serrate, or just undulate; inner margins entire or with tiny teeth. Lobes of lateral leaflets relatively wide at base, tapering to a thin acuminate apex. Venation craspedodromous-camptodromous. Secondary veins ending in the marginal teeth or, when the margin is entire, anastomosing.

R e m a r k s. The compound leaves of this species were originally described from Sośnica by Göppert (1855) as *Rhus aegopodifolia* and *Rhus quercifolia.* None of the original specimens from Göppert's collection, illustrated in the publication, has survived. The first to identify them as *Acer* leaves was Baykovskaya, as mentioned by Shvaryova (1965) in her publication and subsequently confirmed by Il'inskaya (1968). Of the two Göppert's species names, Baykovskaya chose „*aegopodifolium*" to avoid confusion with another archaic *Acer* species named "*quercifolium*" (Il'inskaya op. cit.).

Acer aegopodifolium is so far known only from the upper Neogene of central Europe. Imparipinnate leaves were in the past associated with the genus *Rhus* (Göppert 1855), or

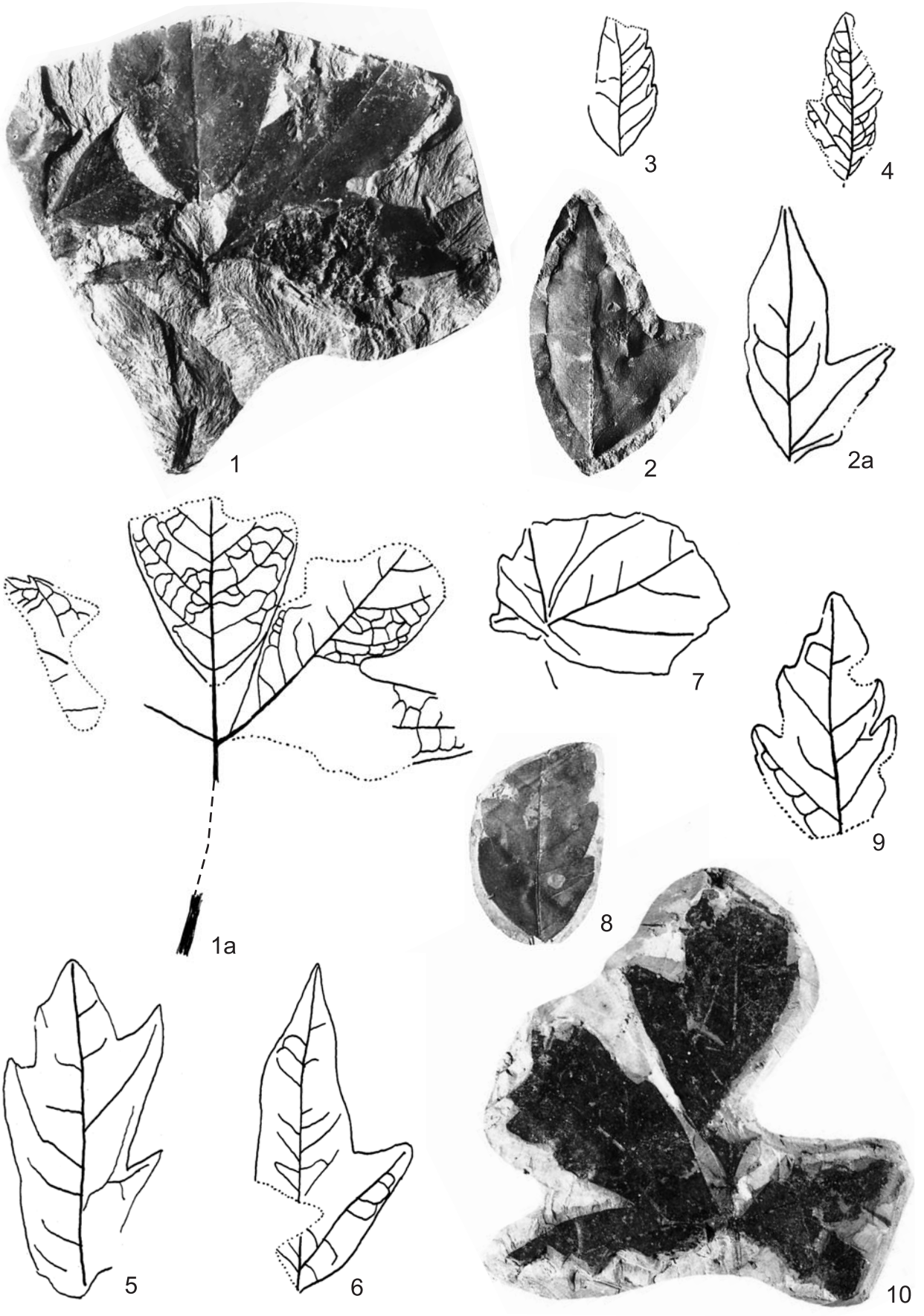


Fig. 9. *Acer aegopodifolium* (Göpp.) Bajkovskaja ex Iljinskaja. **1, 1a –** KRAM-P 54/299; **2, 2a** – MGUWr 655p/1; **3** – KRAM-P 54/976; **4** – MGUWr 554p; **5** – MGUWr 962p/2; **6** – MGUWr 962p/3/II; **7** – MGUWr 978p/4; **8** – MZ VII/53/235; **9** – MGUWr 664p/3; **10** – neotype, MGUWr 1559p/1. Phot. A. Pachoński

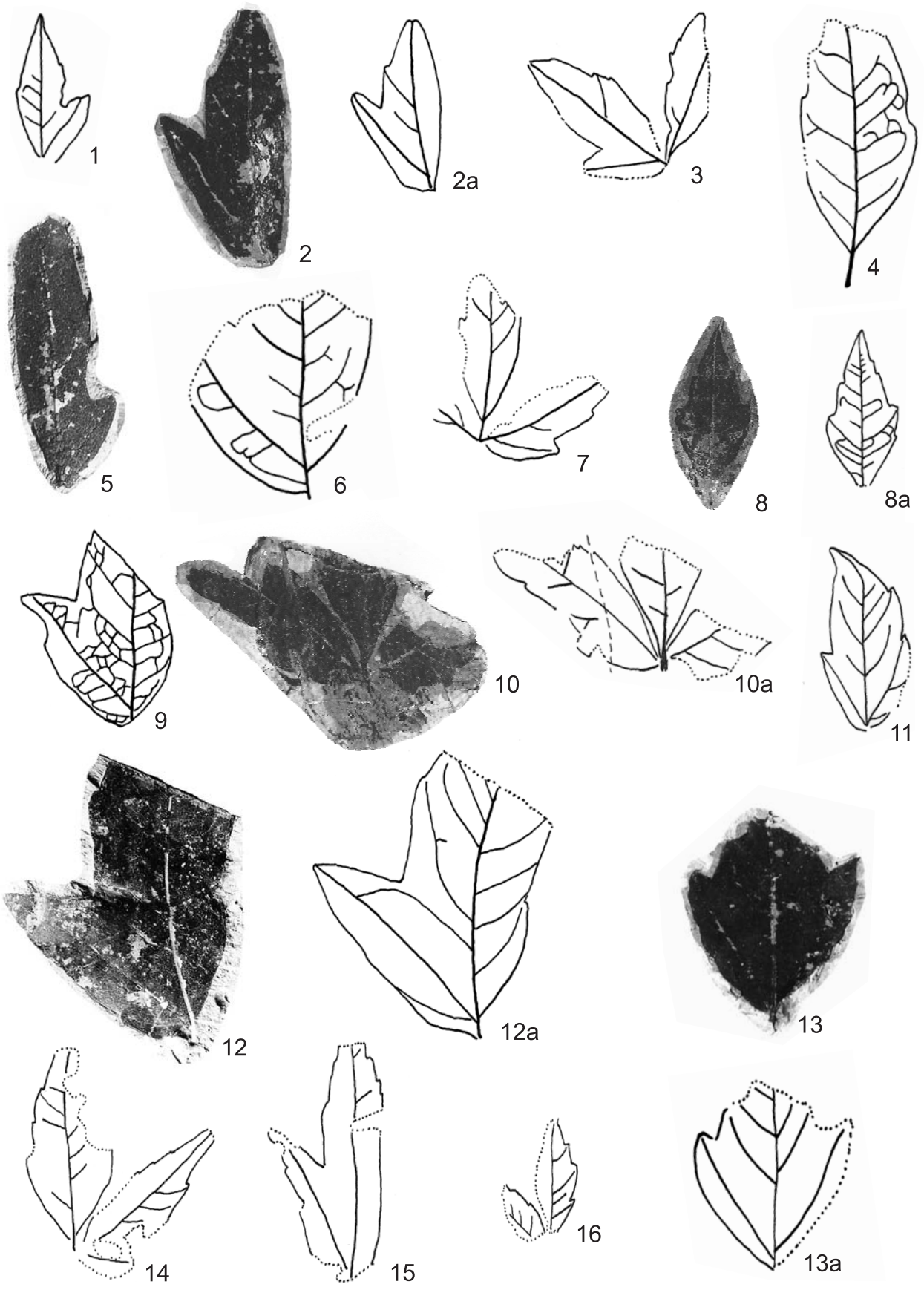


Fig. 10. *Acer aegopodifolium* (Göpp.) Bajkovskaja ex Iljinskaja. **1** – MGUWr 1015p/14; **2, 2a** – MGUWr 1559p/3; **3** – MGUWr 2037p; **4** – MGUWr 2315p/II; **5** – MGUWr 1910p; **6** – MGUWr 2051p; **7** – MGUWr 2283p/I; **8, 8a** – IG 46.III.128; **9** – MGUWr 539p/1/II; **10, 10a** – IG 46.III.129; **11** – MGUWr 220p; **12, 12a** – KRAM-P 54/298; **13**, **13a** – MGUWr 2364; **14** – MGUWr 1559p/5; **15** – MGUWr 1559p/4; **16** – MGUWr 1559p/2. Phot. A. Pachoński

Monopleurophyllum Andreánszky (Andreánszky 1959). It was not until the mid 20th century that these leaves were classified, on the basis of their morphology, as belonging to the genus *Acer* L. (e.g. Baykovskaya in Shvaryova 1965, Baykovskaya in Il'inskaya 1968). Schmitt & Z. Kvaček (1999) were the first to provide data on the cuticle structure of the fossil species from material found in the late Miocene flora of Hambach.

Contemporary species from sect. *Trifoliata* Pax are comparable with the fossil species. A similar epidermis structure is present in some other species, *Acer griseum* (Franchet) Pax and *A. trifolium* Komarov, from the series *Grisea* Pojarkova (Schmitt & Z. Kvaček 1999). Leaf anatomy in contemporary species from sect. *Trifoliata* Pax was examined also by Ströbitzer-Hermann (2002) who found a similar epidermis structure (abaxial epidermis) in *A. mandshuricum* Maximowicz, sect. *Trifoliata*, series *Mandshurica* Pojarkova, which, however, differed morphologically.

Acer aegopodifolium is one of the rarest Tertiary maple species, known so far only from the Middle and Upper Miocene of central and eastern Europe. As far as is presently known it was an accesory species in azonal forest communities.

Acer campestrianum Dorofeev

Fig. 11: 2–4

1855 Fructus *Aceris*; Göppert, p. 34, Pl. 24, figs 7 (missing), 8 (MGUWr 868p).

1919 *Acer trilobatum* (Sternb.) A. Br.; Meyer, p. 169, Pl. 15, fig. 9.

1977 *Acer campestrianum*; Dorofeev, p. 70, Pl. 12, figs 2–4.

1954 *Acer palaeo-Miyabei* Mädler; Szafer, p. 45, Pl. 10, fig. 14.

Material. MGUWr 653p/1, 653p/2/I (with twin impression 653p/3), 868p, 953p/4; four impressions of fruit, one with twin impression.

Description. Fruits winged. Endocarps semi-circular measuring 7.5 × 6.5, 8.0 × 7.5 and 9.0 × 7.6 mm, length (including wings)

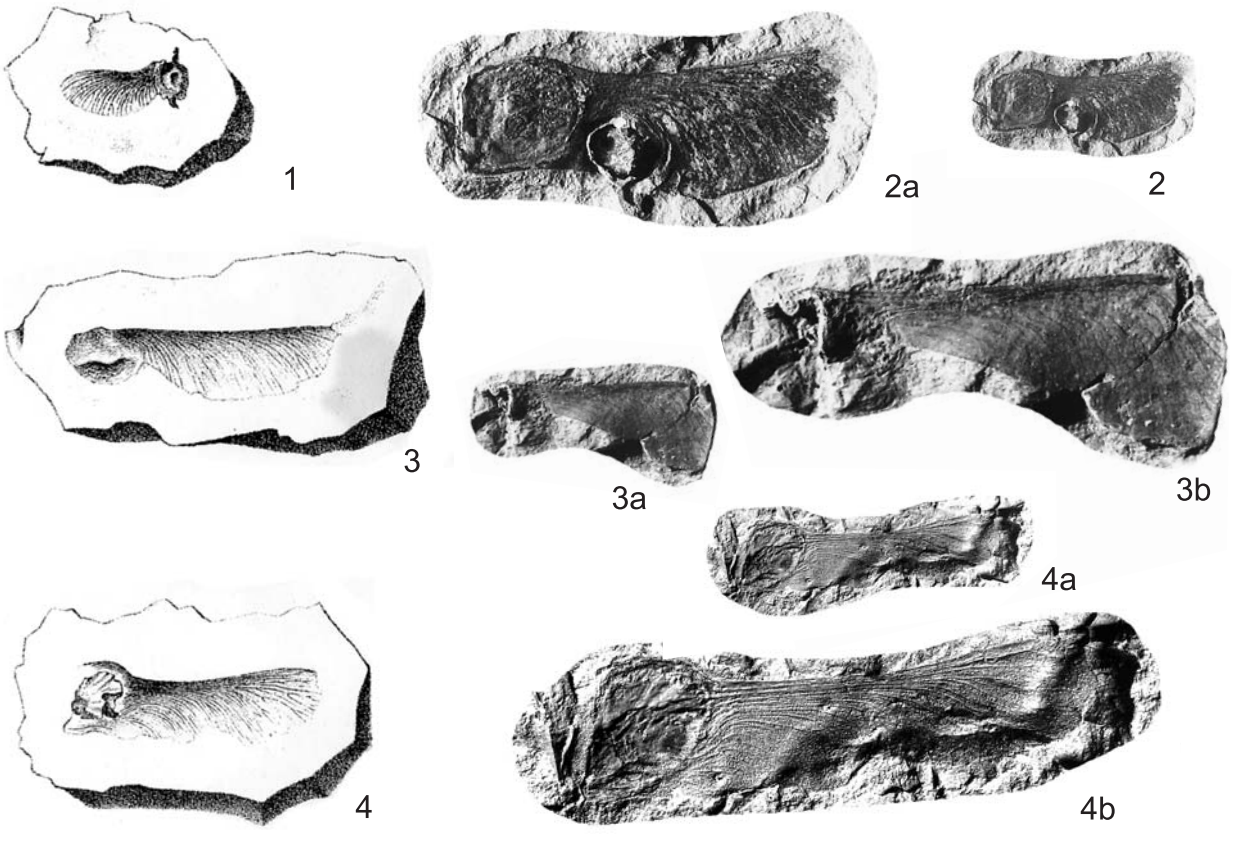


Fig. 11. 1 – *Acer* sp. – fruit, as fructus *Aceris*, Göppert 1855, Pl. 24, fig. 9; *Acer campestrianum* Dorofeev – fruits: **2** – MGUWr 653p/2/I (with an impression of *Eoeuryale* seed without operculum), **2a** – ×2; **3** – as fructus *Aceris*, Göppert 1855, Pl. 24, fig. 7, **3a** – MZ VII/7/6, **3b** – ×2; **4** – as fructus *Aceris*, Göppert 1855, Pl. 24, fig. 8, **4a** – MGUWr 868p, **4b** – ×2. Phot. A. Pachoński

Table 1. The results of revision of the *Acer* taxa based on Göppert's original specimens from Sośnica

Taxon	Göppert's (1855) illustration	Specimen number	Current determination
Acer subcampestre Göpp.	Pl. 22, figs 16,17	missing	*Acer subcampestre* Göpp.
Acer ribifolium Göpp.	Pl. 22, fig. 18	missing	*Acer tricuspidatum* Bronn
Acer ribifolium Göpp.	Pl. 22, fig. 19	missing	undetermined
Acer strictum Göpp.	Pl. 23, figs 1–3,5	missing	*Vitis stricta* (Göpp.) Knobloch
Acer strictum Göpp.	Pl. 23, fig. 4	MGUWr No. 805p	*Vitis stricta* (Göpp.) Knobloch
Acer triangulilobum Göpp.	Pl. 23, fig. 6	missing	*Vitis stricta* (Göpp.) Knobloch
Acer hederaeformis Göpp.	Pl. 23, figs 7–10	missing	*Liquidambar europaea* A. Br.
Acer oeÿnhausianum Göpp.	Pl. 24, figs 1,2,4	missing	*Liquidambar europaea* A. Br.
Acer oeÿnhausianum Göpp.	Pl. 24, fig. 3	MGUWr No. 822p/1	*Liquidambar europaea* A.Br.
Acer cÿtisifolium Göpp.	Pl. 24, figs 5,6	missing	*Liquidambar europaea* A.Br.
Fructus *Aceris*	Pl. 24, fig. 7	missing	*Acer campestrianum* Dorof.
Fructus *Aceris*	Pl. 24, fig. 8	MGUWr No. 868p	Acer campestrianum Dorof.
Fructus *Aceris*	Pl. 24, fig. 9	missing	*Acer* sp.
Semen *Aceris*	Pl. 24, fig. 10	missing	non *Acer*, undetermined

2.5–3.5 cm. Septum dividing the two wings straight, perpendicular to the fruit margins.

Remarks. The species was described by Dorofeev (1977) from the Pliocene of Simbugino from Bashkiria; it occurred also in the Pliocene of Mizerna (Szafer 1954) and Germany (Mai & Walther 1988). It represents fruits of a maple belonging to the series *Campestria* (Pax) Pojarkova in sect. *Platanoidea* Pax, comparable with the recent *A. campestre* L. (Dorofeev op. cit.).

Acer sp. div.?

Fig. 11: 1

Material. MGUWr 687p/7, 825p/I, 953p/2, 953p/3, 5122p, 5134p, KRAM-P 54/5/IV, 54/29/II; MZ VII/53/6; nine impressions of parts of fruits.

Remarks. The impressions represent fragments of wings of *Acer* fruits. Their identification to species is impossible because the endocarps are lacking. Perhaps some of them belong to *A. campestrianum* Dorof., but at least one (Fig. 11: 1) represents a different *Acer* species, on account of the different shape of the wing.

CONCLUSIONS

In the late Miocene flora of Sośnica occur leaves belonging to five *Acer* species: *Acer vindobonense* (Ettinsh.) Berger from sect. *Palmata* Pax, *Acer tricuspidatum* Bronn from sect. *Rubra* Pax, *Acer subcampestre* Göpp., *A. integrilobum* Weber sensu Walther from sect. *Platanoidea* Pax, and *Acer aegopodifolium* (Göpp) Baykovskaya ex Iljinskaya from sect. *Trifoliata* Pax (Table 1). They are accompanied by fruit remains, some of which have been identified as *Acer campestrianum* Dorof. from sect. *Platanoidea* Pax. The trees would not have been numerous. As elsewhere in Neogene vegetation of Europe, they constituted only an admixture in Neogene mesophytic deciduous and mixed forest.

All the distinguished *Acer* species are known from the Neogene floras of Europe, with *Acer tricuspidatum* Bronn the most common.

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