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DOI: 10.2478/fbgp-2014-0001

THE WHOLE PLANT RECONSTRUCTION OF *BANISTERIAECARPUM GIGANTEUM* AND *BYTTNERIOPHYLLUM TILIIFOLIUM* - A PRELIMINARY REPORT

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Key words: Fossil Malvaceae; Europe; middle Miocene to Pliocene; fruits; foliage

Abstract: *New records of fruits of Banisteriaecarpum giganteum (Göppert) Kräusel from the middle and late Miocene of Austria and Hungary and the Pliocene of Romania regularly associated with foliage of Byttneriophyllum tiliifolium (A. Braun) Knobloch & Kvaček confirm previous views of Czeczott, Ţicleanu and others that the two organs belong to a single plant related to Malvaceae s.l. and not to Mapighiaceae, as previously assumed by Schenk, Kräusel and Kirchheimer. According to the fruit morphology it is closely similar to Tarrietia Blume (tropical SE Asia and Africa, sometimes included together with Argyrodendron F. Muel. to Heritiera Dryand. in Ait.), with which it partly shares habitats (swamp to riparian forests) and decidedly differs in foliage (leaves strongly asymmetric ovate vs symmetric simple ovate to elongate or palmately compound) and climatic requirements (warm temperate vs tropical conditions). Its pollen has not yet been firmly discriminated. The fossils so far assigned to Tarrietia from Europe must be excluded from this genus: Tarrietia hungarica Rásky from the early Oligocene of Hungary was assumed by Andreánszky as legume fruits (Machaerites hungaricus (Rásky) Andreánszky), Tarrietia germanica Rüffle from the early Miocene of Germany, according to fine venation pattern, may also represent a monospermic legume pod.*

INTRODUCTION

The whole plant concept in palaeobotany has lately attracted much interest of those working mainly with megafossil remains of various ages (see e.g. Kvaček, 2005, 2008). Until we are able to recognize individual whole plants in the fossil record we can hardly fully understand diversity of ancient plant world and the significance of plant elements for palaeoenvironmental reconstructions.

In this preliminary paper we bring one example of the whole plant concept represented by the "giant maple" *Banisteriaecarpum giganteum* (Göppert) Kräusel, a characteristic extinct plant element of the Cenozoic of Eurasia and discuss its systematic affinities and nomenclature. Our report precedes a wider revision requiring inspection of more records from Eurasia. This research was initiated by late Nicolae Ţicleanu, former professor of the University of Bucharest, who collected with other Romanian explorers (Ţicleanu, 1982) most complete series of the fruits treated in this paper and invited us to cooperate, but was unable to finish our study. Independently from this study, a wider monograph on the malvalean Neogene foliage and co-occurring pollen was published in cooperation with Grzegorz and ElżbietaWorobiec, Kraków (Worobiec et al., 2010) and another monograph of the late Miocene flora of Hungary containing *Banisteriaecarpum* (Hably, 2013).

MATERIAL AND METHODS

The studied material of *Banisteriaecarpum giganteum* includes either fruit impressions without traces of lignified matter preserved in sandy or silty oxidized layers (Hungarian Pannonian of Rudabánya-Vilmos, Austrian middle Miocene of Graz-Andritz – see Hably, 2013) or, more importantly, compressions with preserved lignified tissue allowing epidermal studies (Romanian Pliocene of Bălteni, Lupoaia – see Ţicleanu, 1989). The co-occurring fossil foliage of *Byttneriophyllum tiliifolium* is similar in its preservation mode, i.e. both

impressions and lignified compressions. Preliminary attempts to macerate pericarp tissue of the fruits (Schulze's solution in combination with 10% KOH) yielded only poorly preserved structures and require further preparations. The compression foliage of *Byttneriophyllum* from the Romanian Pliocene has not yet been studied for cuticles. The co-occurring pollen at Rudabánya and Lupoaia was explored separately earlier (E. Worobiec in Worobiec et al., 2010). Most of the studied fossil material is housed in the Hungarian Geological and Geophysical Institute, Budapest (BK), Hungarian Natural History Museum, Budapest (BP), University of Bucharest (UBUC), Institut für Botanik, Karl-Franzens-Universität in Graz, (UGR) and Landesmuseum Joanneum, Graz (JOAN).

We devote much attention to comparisons with possible living relatives, which we studied in several herbaria, i.e. Hungarian Natural History Museum, Budapest (BP), Muséum d'Histoire naturelle, Paris (P), Charles University in Prague (PRC) and in the field in Hainan.

RESULTS

Previous views

These maple-like fruits were originally described by Göppert (1852) from the Polish Neogene limestone at Stróza (in German Striese). Göppert named them as *Acer giganteum* Göppert (1852, p. 279, pl. 38, figs 1a-c, 2, 3). Because of the large size of fruits he considered a connection with associated foliage not fitting into any species of maple and assigned the foliage to *Dombeyopsis* Unger. In the same work Göppert named a smaller specimen of fruits as *Acer otopteris* Göppert (1852, p. 279, pl. 38, fig. 4). For the latter he believed to belong to a maple but he also admitted that such fruits are similar to winged fruits of the Malpighiaceae, namely *Heteropterys chrysophylla* (Lamarck) Kunth. Later Unger (1856, pp. 29-30) assumed that such single-seeded fruits from Austrian middle Miocene at Prävali may partly represent pods of legumes of *Centrolobium* Martius ex Bentham and named them *Centrolobium giganteum* (Göppert) Unger. Schenk (1890) directly interpreted these fossils to belong to disintegrated fruits of the Malpighiaceae Juss., namely the genus *Banisteria* L. (now a synonym of *Heteropterys* H.B.K., nom. cons. and *Banisteriopsis* C.B. Rob. & Small) from American tropics. Kräusel (1951) summarized all previous views and preferred to establish for fruits a fossil genus *Banisteriaecarpum* of the Malpighiaceae because in his opinion it would be difficult to decide, to which genus of this family the fruits really belong. This concept was also accepted by Kirchheimer who lists most of the so far known records (Kirchheimer, 1957, pp. 82, 652).

Czeczott (1967) stated differences between fruits of *Banisteriaecarpum* and *Banisteria* and noted regular co-occurrence of *Banisteriaecarpum* with strongly asymmetric leaves of "*Ficus*" *tiliaefolia* (A. Braun) Heer (= *Byttneriophyllum tiliifolium* (A. Braun) Knobloch & Kvaček). She was the first who questioned affinities to Mapighiaceae and suggested possible relationship to Sterculiaceae (DC.) Bartl. (= Malvaceae Juss. subfam. Sterculioideae Beilschm.).

Ţicleanu (1982) recovered with other colleagues the most complete collection of *Banisteriaecarpum* fruits in the Romanian Pliocene. Endeavoring the whole plant designation, he later (Ţicleanu, 1989) created a parallel new name combination *Byttneriophyllum giganteum* (Göppert) Ţicleanu, besides *Byttneriophyllum tiliifolium*, in order to unite the two organs into a single fossil genus with two species. This solution has not been followed (Hably & Kovar-Eder, 1996; Hably 2013) and is not in line with current nomenclatural rules (see below).

Nomenclature

Two fossil genera have been used for naming disconnected fruits and foliage: *Banisteriaecarpum* Kräusel (1951) typified by *B. giganteum* (Göppert) Kräusel and *Byttneriophyllum* Givulescu ex Knobloch & Kvaček (1965a, b) typified by *Byttneriophyllum tiliifolium* (A. Braun) Knobloch & Kvaček. The latter was superfluously replaced by *Braunia* Givulescu (1970) – see Jähnichen (1984). Hence the combination *Braunia tiliaefolia* (A. Braun) Givulescu is illegitime and cannot be employed for both fruits and foliage, as proposed by Ţicleanu (1982). Also it is not in line of the nomenclatural code to accept the combination *Byttneriophyllum giganteum* (Göppert) Ţicleanu (1989) because *Banisteriaecarpum* was published earlier (Kräusel, 1951) than *Byttneriophyllum* Givulescu ex Knobloch & Kvaček 1965a and should be given priority.

Banisteriaecarpum papilio Andreánszky (1955, p. 43, fig. 4) from the Hungarian Oligocene should be removed from this fossil genus because it clearly deviates from the concept suggested by Kräusel (1951) and requires a separate detailed revision.

Plate I.

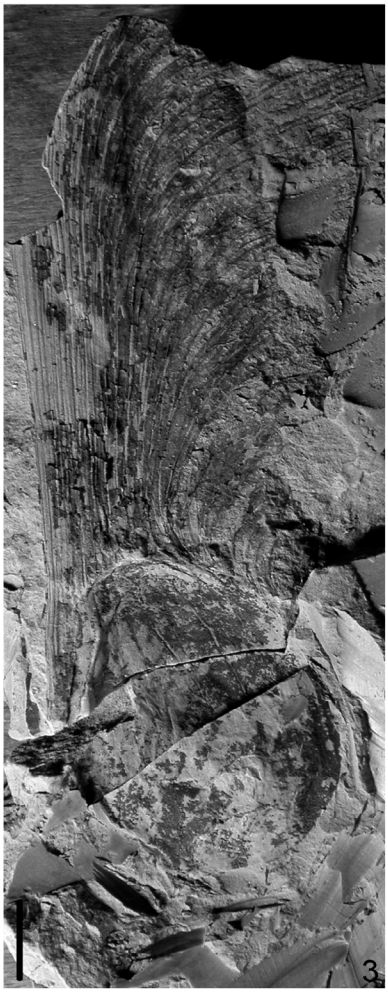
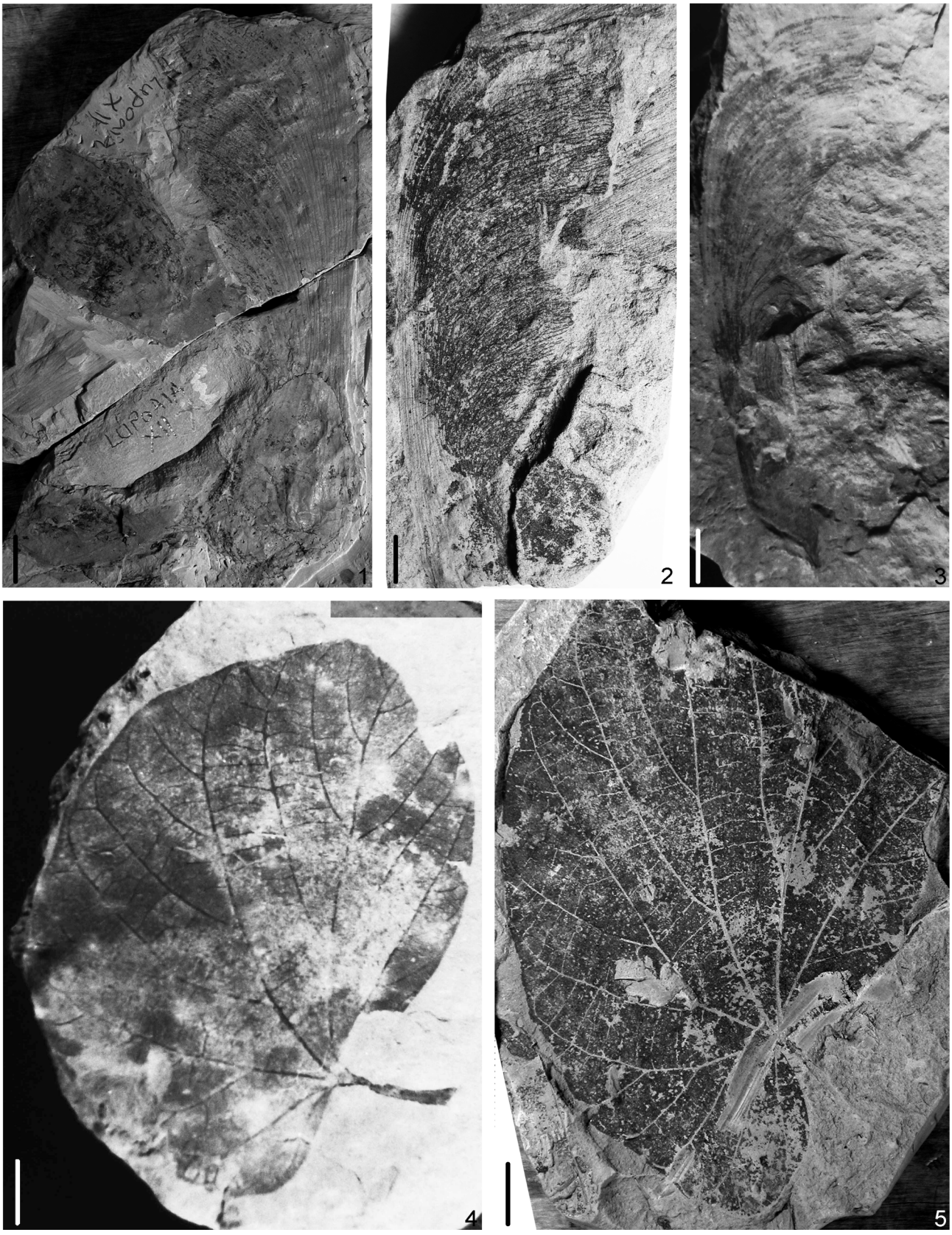


Plate II.



PROPOSED INTERPRETATION OF THE *BANISTERIAECARPUM GIGANTEUM - BYTTNERIOPHYLLUM TILIIFOLIUM* PLANT

Fruits

New records of fruits of *Banisteriaecarpum giganteum* (Plate I, figs 1-4; Plate II, figs 1-3) from the middle and late Miocene of Austria and Hungary (Hably, 2013) and the Pliocene of Romania (Ţicleanu, 1982) were found regularly associated with the foliage of *Byttneriophyllum tiliifolium* (Plate II figs 4-5). Thus they confirm previous views of Czeczott (1967), Ţicleanu (1989) and others that the two organs belong to a single plant related to Malvaceaes s.l. and not to Mapighiaceae, as assumed by Schenk (1890), Kräusel (1951) and Kirchheimer (1957).

According to the fruit morphology this plant is closely similar to *Tarrietia* Blume (Pl. 3, figs 7-9) distributed in tropical SE Asia, sometimes merged with *Heritiera* Dryand. in Ait. together with *Argyrodendron* F. Muell. (Kostermans, 1959), with which it partly shares habitats (swamp to riparian forests) and decidedly differs in foliage (leaves strongly asymmetric ovate vs symmetric ovate-elongate, simple or palmately compound) and climatic requirements (warm temperate vs tropical conditions).

More detailed study will be accomplished in the future, but first attempts to get epidermal pericarp structure of *Banisteriaecarpum* fruits are promising showing some important features, such as bases of stellate trichomes on the surface. Fossils referred to *Banisteriaecarpum giganteum* from East Asia (Fotjanova, 1988; Ozaki, 1991; Chen Yun-fa, personal communication 2014) require also further studies.

Foliage

First descriptions of foliage which we assume to belong to *Banisteriaecarpum*, were published as *Cordia tiliifolia* A. Braun (1845, p. 170) from the middle Miocene of Öhningen. Göppert (1852) assigned such leaf fossils co-occurring with his *Acer giganteum* to the fossil genus *Dombeyopsis* Unger under three species *D. tiliifolia* (A. Braun) Unger, *D. grandifolia* Unger and *D. aequalifolia* Göppert. Different views on affinities of this peculiar morphotype stems from an unusual asymmetric form of the leaf lamina and venation. The epidermal study by Knobloch and Kvaček (1965a, b) denied its inclusions into the genera *Cordia* (Braun 1845), *Ficus* (Heer, 1856), *Alangium* (Kryshtofowich, 1937; Iljinskaya, 1968) and suggested most acceptable solution to treat it in a separate fossil genus *Byttneriophyllum* following the concept proposed by Givulescu (1959). A more thorough epidermal study (Worobiec et al., 2010) summarized previous interpretations and confirmed this concept treating *Byttneriophyllum* foliage as a part of the plant bearing *Banisteriaecarpum* fruits.

Pollen

Connection with the dispersed pollen has not been resolved so far. Worobiec et al. (2010) attempted to fix the relationship of various malvalean morphotypes used for foliage (*Dombeyopsis lobata* Unger, *Byttneriophyllum tiliifolium* (A. Braun) Knobloch & Kvaček, "*Ficus*" *truncata* Heer) with dispersed pollen types and sampled layers, where foliage of *Byttneriophyllum tiliifolium* abundantly occurred. In samples from Rudabánya and Lupoaia, where even fruits of *Banisteriaecarpum* are present, single specimens of *Intratriporopollenites insculptus* Mai were encountered while at Belchatów in asso-

Plate I, figs 1-4. *Banisteriaecarpum giganteum* (Göppert) Kräusel; 1) A group of detached fruits, Lupoaia, Pliocene, NT-L281b (UBUC), scale bar 10 mm; 2) Seed part with curved neck and distinct venation of wing. Lupoaia, Pliocene, NT-L278(2) (UBUC), scale bar 10 mm; 3) Seed part with carbonized pericarp. Lupoaia, Pliocene, NT-L279 (UBUC), scale bar 10 mm; 4) Incomplete fruit with distinct venation of wing. Bălteni, Pliocene, NT-L282 (UBUC), scale bar 10 mm.

Plate II, figs 1-3. *Banisteriaecarpum giganteum* (Göppert) Kräusel; 1) A group of big fruits, Lupoaia, Pliocene, NT-L280 (UBUC), scale bar 10 mm; 2) Almost complete fruit, Rudabánya, late Miocene, BK 554 (BK), scale bar 10 mm; 3) A complete fruit with straight neck, Graz-Andritz, middle Miocene, Pb 17.10 (UGR), scale bar 10 mm; figs 4-5. *Byttneriophyllum tiliifolium* (A. Braun) Knobloch & Kvaček; 4) Petiolate leaf impression, Graz-Andritz, middle Miocene, Pb 17.10 (UGR), scale bar 10 mm; 5) Carbonized compression, Lupoaia, Pliocene, NT-L283 (UBUC), scale bar 10 mm.

ciation of *Byttneriophyllum* foliage the pollen of the *Intratriporopollenites instructus* type occurred. E. Worobiec (in Worobiec et al., 2010, p. 910) stated: "For the fossil leaf morphogenus *Byttneriophyllum*, an appropriate pollen type has not been discriminated, but pollen grains of *I. instructus* often accompanied these leaves." Fossil flowers in association with the *Banisteriaecarpum - Byttneriophyllum* plant have not been recovered so far even in the sub-autochthonous assemblages. Krutzsch (2004) treated in detail the above-mentioned "tilioid" pollen taxa but unfortunately left aside comparisons with pollen of the Sterculioideae.

Affinities to modern angiosperms

Maple-like winged fruits are produced in various groups of eudicots (Kirchheimer, 1957, p. 34). Indeed, disintegrated double samaras of Acer (Plate III, figs 1-2) and the Malpighiaceae (Plate III, figs 3-5) may look similar to *Banisteriaecarpum*. On account of foliage and its epidermal micromorphology the *Banisteriaecarpum - Byttneriophyllum* plant must be related to the Malvaceae s.l. (Knobloch & Kvaček, 1965a, b; Worobiec et al., 2010). Anomocytic stomata, stellate trichomes and glandular multicellular clavate trichomes suggest affinities with the subfamilies Tilioideae Arn. or Brownlowioideae Burret (G. Worobiec in Worobiec et al., 2010) while the fruit morphology is leading to the Sterculioideae Beilschm. (Czeczott, 1967; Ţicleanu, 1982, 1989). The complete samara of *Heritiera* (Plate III, fig. 6) differs considerably by its globose form but the winged fruits of *Tarrietia* match *Banisteriaecarpum* in many respects (Plate III, figs 7-9). However, we did not find any living relative producing similar foliage (cf. Plate III, figs 10-12). In our opinion it is necessary to recognize other organs, namely dispersed pollen, and carry out detailed palynological studies in order to resolve exact position of the *Banisteriaecarpum - Byttneriophyllum* plant within the Malvaceae s.l. Also a recovery of wood, possibly belonging to this extinct element, would be of great importance.

FOSSILS EXCLUDED FROM THE MALVACEAE S.L.

Rásky (1950) described a winged disseminule from the early Oligocene of Hungary (locality Budaújlak), which she interpreted as a samara of *Tarrietia* (*T. hungarica* Rásky) (Plate IV, fig. 1). Some other specimens collected from the same site (Plate IV, figs 2-5) were assumed by Andreánszky (1962, p. 228, 1965, p. 67) as legume fruits (*Machaerites hungaricus* (Rásky) Andreánszky). According to S.R Manchester (personal communication 2014), also seeds of some Anacardiaceae (*Schinopsis* Engl.) are comparable.

A fruit interpreted as belonging to *Tarrietia* was described from the early Miocene of the Randeck Maar, Germany as *Tarrietia germanica* Rüffle (1963, p. 247, pl. 14. fig. 17, pl. 27, fig. 8). We observed on the holotype fine venation pattern characteristic of legume pods (Plate IV, fig. 6) proving that this fossil may represent a legume fruit and not that of *Tarrietia* nor *Koelreuteria* Laxmann, as Gregor (1986, p. 11) suggested.

CONCLUSIONS

New records of fruits of *Banisteriaecarpum giganteum* accompanied by foliage of *Byttneriophyllum tiliifolium* from the Miocene of Austria, Hungary and the Pliocene of Romania confirm previous views of Czeczott (1967), Ţicleanu (1982, 1989), Worobiec et al. (2010), Hably (2013) and others that the two organs belong to a single plant related to Malvaceae s.l. and not to Mapighiaceae.

The *Banisteriaecarpum giganteum – Byttneriophyllum tiliifolium* plant is closely similar in fruits to *Tarrietia* Blume (mainly tropics in SE Asia) with which it shares partly also similar habitats (swamp to riparian forests) but decidedly differs in foliage and climatic requirements (warm temperate vs tropical conditions).

Fossils assigned to *Banisteriaecarpum giganteum* and associated with foliage similar to *Byttneriophyllum tiliifolium* were also recorded from the Cenozoic of East Asia, e.g. Sakhalin (Fotjanova, 1988), Japan (Ozaki, 1991) and China (Chen Yunfa, personal communication). The relevant material was only partly accessible for the present account and requires further studies.

Fossil fruits so far assigned to *Tarrietia* from Europe must be excluded from this genus probably representing legume pods.

Plate III.

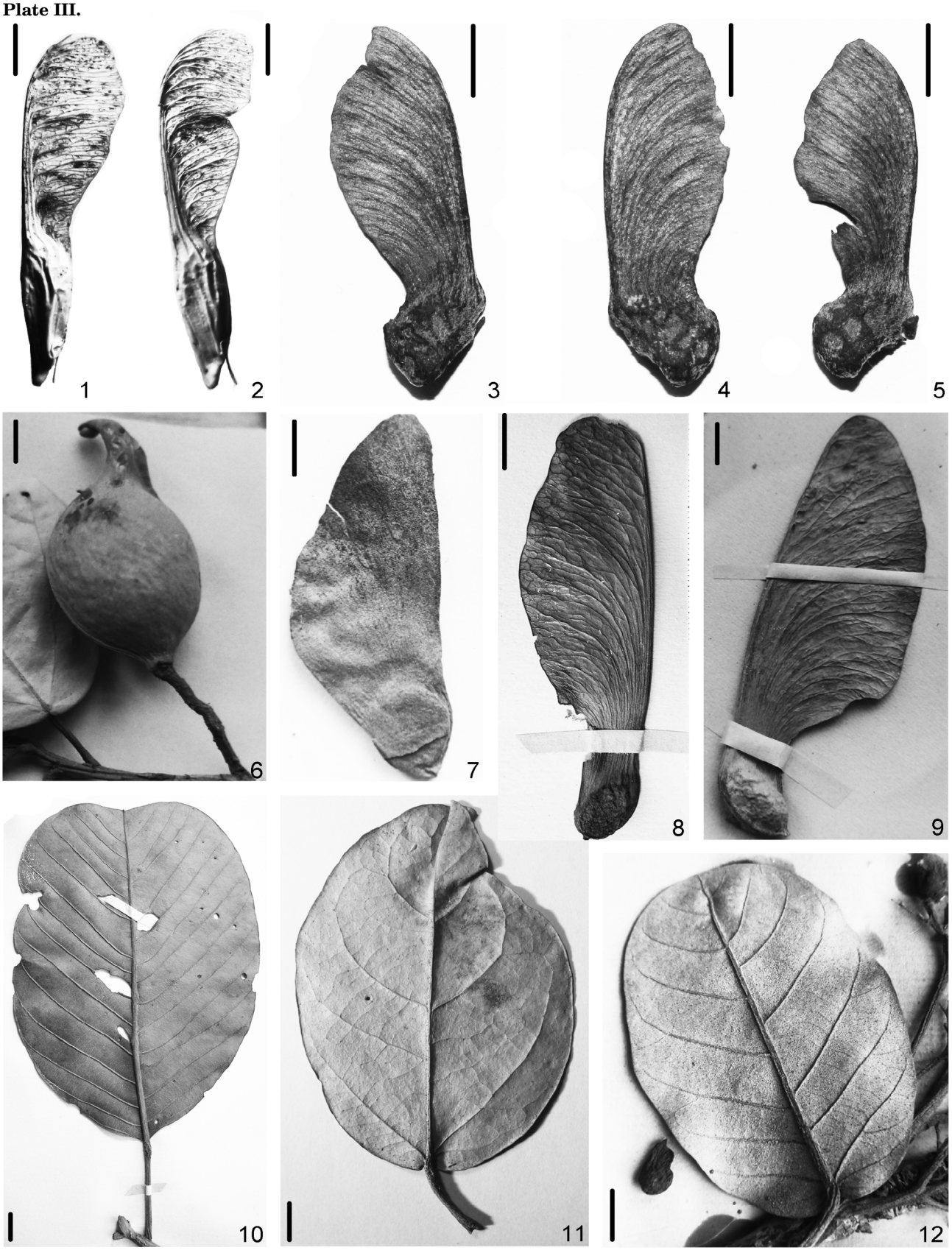


Plate IV.

Plate IV, figs 1-5. "*Tarrietia*" *hungarica* Rásky (=*Machaerites hungaricus* (Rásky) Andreánszky), Budaújlak, early Oligocene of Hungary; 1) Type specimen, BP 55.2199.2, scale bar10 mm; 2) Incomplete fruit showing venation, BP 55.2200.1, scale bar 10 mm; 3) Fruit with seed part, BP 56.2197.2, scale bar 10 mm; 4) Counter-impression of the previous specimen, BP 56.2197.2, scale bar 10 mm; 5) Small fruit, BP 55.2198.2, scale bar 10 mm; 6) "*Tarrietia*" *germanica* Rüffle, holotype, Randeck Maar, middle Miocene, P 1224/588, Staatliches Museum für Naturkunde, Stuttgart, scale bar 10 mm.

Plate III, figs 1-2. *Acer negundo* L., separate parts of double samara, cult. Praha-Bohnice, scale bars 5 mm; 3-5. *Heteropterys bellonis* Urb., separate parts of double samaras, Porto Rico, Sabaun Grande, *Sintenis* 3892 (PB), scale bars 5 mm; 6) *Heritiera percoriacea* Kosterm., globular fruit, SW Java, Udhung Kulon, *Kostermans* 14100 (P), scale bar 5 mm, 7) *Tarrietia parvifolia* (Merr.) Merr.& Chun, small winged fruit, Hainan, Yaichow, *How 71047* (P), scale bar 5 mm; 8) *Tarrietia symplicifolia* Mast., winged fruit, N. Borneo, *Enggoh 7138* (P), scale bar 10 mm; 9) *Tarrietia javanica* Blume, winged fruit, Cambodia, *Bijeaud sine num*. (P), scale bar 10 mm; 10) *Tarrietia symplicifolia* Mast., leaf, N. Borneo, *Enggoh 7138* (P), scale bar 10 mm; 11) *Heritiera cordata* Kosterm., leaf, Annam, *Poilane 4950* (P), scale bar 10 mm; 12) *Tarrietia parvifolia* (Merr.) Merr.& Chun, leaf, Hainan, Dongzhai Gang, *Kvaček Z. sine num. March* 6, 2009 (PRC), scale bar10 mm.

ACKNOWLEDGMENTS

This study is a continuation of our research of Tertiary floras, in which we cooperated with many colleagues in Europe since long. It is most unfortunate that the initiator of this project, prof. Nicolae Ţicleanu, University of Bucharest, died before the project was completed. We thank G. and E. Worobiec, Kraków for cooperation in epidermal and pollen studies. We owe sincere thanks to a number of people and institutions for giving us opportunity to study the relevant fossil as well modern material: J. Kovar-Eder, Staatliches Museum für Naturkunde, Stuttgart, V. Parashiv, University of Bucharest, I. Rácz, Hungarian Natural History Museum, Budapest and curators of the herbaria in the Museum d' Histoire naturelle, Paris, Faculty of Science of Charles University, Prague and of the collections of the Landesmueum Joanneum, Graz, and the Botanical Institute of the Graz University for assistance; Prof. Li Cheng-sen, Beijing, guided the first author to a field trip in Hainan; Barbara Mohr, Berlin kindly accepted our report as a lecture to the program of the 23rd International Workshop on Plant Taphnonomy, Berlin, Nov. 27-28, 2014. Steven R. Manchester, Florida Museum, Gainesville corrected the manuscript linguistically, Vasilis Teodoridis critically reviewed the text and helped with illustrations. The research was carried out and financially supported by the Ministry of Education, Youth and Sports of the Czech Republic (project No. PRVOUK P 44), the Grant Agency of the Czech Republic (GA ČR project No.14-23108S) and Hungarian Scientific Research Fund (OTKA 108664).

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