Early Miocene records of *Craigia* (Malvaceae s.l.) in the Most Basin, North Bohemia – whole plant approach

Spodnomiocenní doklady rodu *Craigia* (Malvaceae s.l.) v mostecké pánvi v severních Čechách – celostní přístup

(6 figs)

ZLATKO KVAČEK

Charles University, Faculty of Science, Institute of Geology and Palaeontology, Albertov 6, CZ-128 43 Praha 2, Czech Republic; kvacek@natur.cuni.cz

Fossil records of *Craigia bronnii* (Malvaceae, Tilioideae) including fruits, flower buds and a flower as well as associated foliage of *Dombeyopsis lobata* are summarised from the Early Miocene Most Basin, northern Bohemia, the type area of the species. The typification and local synonymies are provided. The reconstructed plant is compared with the nearest living relative *Craigia yunnanensis* from southern China and northern Vietnam considering the floral, fruit, and leaf morphology and epidermal anatomy as well as autecology.

Key words: Malvaceae s.l.; northern Bohemia; Early Miocene; taxonomy; sociology

Introduction

The North-Bohemian brown-coal basin, i.e. the Most Basin according to the present geological terminology in the Czech Republic, has yielded the richest fossil record of *Craigia* (Malvaceae s.l.). Its fruits have been long known from the European Tertiary and misidentified with various genera and families (e.g., *Ulmus, Abronia*, Rutaceae, Zygophyllaceae etc.). A wider comparative study resulted in assigning these very characteristic fossils to the genus *Craigia* (Kvaček et al., 1991, 2002), today represented by two relictual species in southern China and northern Vietnam. Reviewing the sieved compression fruit and seed collections left by late Č. Bůžek, the author found a number of unripe fruits and flower buds from the coal facies of the Most Basin. These represent young flowering stages of *Craigia bronnii*, as earlier recognised for the same kind of mesofossils in the Rhenish Miocene (Pingen et al., 2001). *Craigia* occurred in the past throughout the Northern Hemisphere starting with the early Palaeogene in Sakhalin as shown by a wider review prepared by a team of Akhmetiev, Kvaček – Manchester. The present contribution provides a more detailed integrated evaluation of all records of *Craigia* within the Most Basin and a reconstruction of the whole plant based on co-occurrence of the detached organs, as already suggested by Kvaček (1993).

Material and methods

The newly recognised flower buds and immature fruits preserved as carbonised mesofossils were sieved from lignite clay sediments by routine micropalaeontological procedure in labs of the former Central Geological Institute (now Czech Geological Survey), Prague and in the National Museum, Prague (personally by F. Holý). These mesofossils, tentatively identified by Holý and Bůžek as *"Tilia"*, were collected in the 1960s (Bůžek – Holý, 1964) and put aside for later studies. The coal matter is permineralized by pyrite in most cases. Commercial bleach "SAVO" was applied for maceration of a flower bud in order to obtain cuticles and pollen in situ, but this attempt failed. The second specimen macerated by Schulze procedure yielded a few clumps of pollen. Larger fossils representing fruit valves, rarely complete fruits of *Craigia bronnii*, and associated leaf remains of *Dombeyopsis lobata*, are partly coalified compressions allowing preparation of cuticles, which come mostly from the Bílina Mine (see Bůžek et al., 1989 – as *Pteleaecarpum*, Sakala, 2000). Other macrofossils studied are impressions of detached valves, rarely more complete fruits, and leaves, which are preserved in silt, clay or baked rocks.

The records of *Craigia* in the Most Basin belong to the richest of this age in Europe and come from ca. 20 sites, mostly in open-cast mines or cores (Fig. 1). They are concentrated in the Holešice and the lowermost part of the Libkovice Member of the Most Formation, and dated into the middle part of the Early Miocene (lower Burdigalian, Eggenburgian, lower Orleanian), as the underlying mammal faunas of MN 3 zone from the seam base at Ahníkov – Merkur-North mine (MN 3a) and the isolated limestone of Tuchořice (MN 3b) indicate (for details of stratigraphy see Kvaček et al., 2004b).

New collections from the environs of Bílina were gathered by the late Čestmír Bůžek, recently by Zdeněk Dvořák, the author, and their co-workers and friends. This material is mostly housed in the Bílina Mine Headquarters, Bílina (DB), Faculty of Science, Charles University (PRC) and the National Museum, Prague (NM). Material from several other sites from various parts of the basin is also housed in the Geological Survey, Prague (UUG) and the Regional museum, Most (MM). The published type and figured specimens described by previous authors in the 19th century have been recovered mainly in the Hungarian Natural Museum, Budapest (BP), partly in the Geologische Bundesanstalt, Vienna (BA), National Museum, Prague (NM), State Museum of Mineralogy and Geology in Dresden (MMG) and elsewhere.

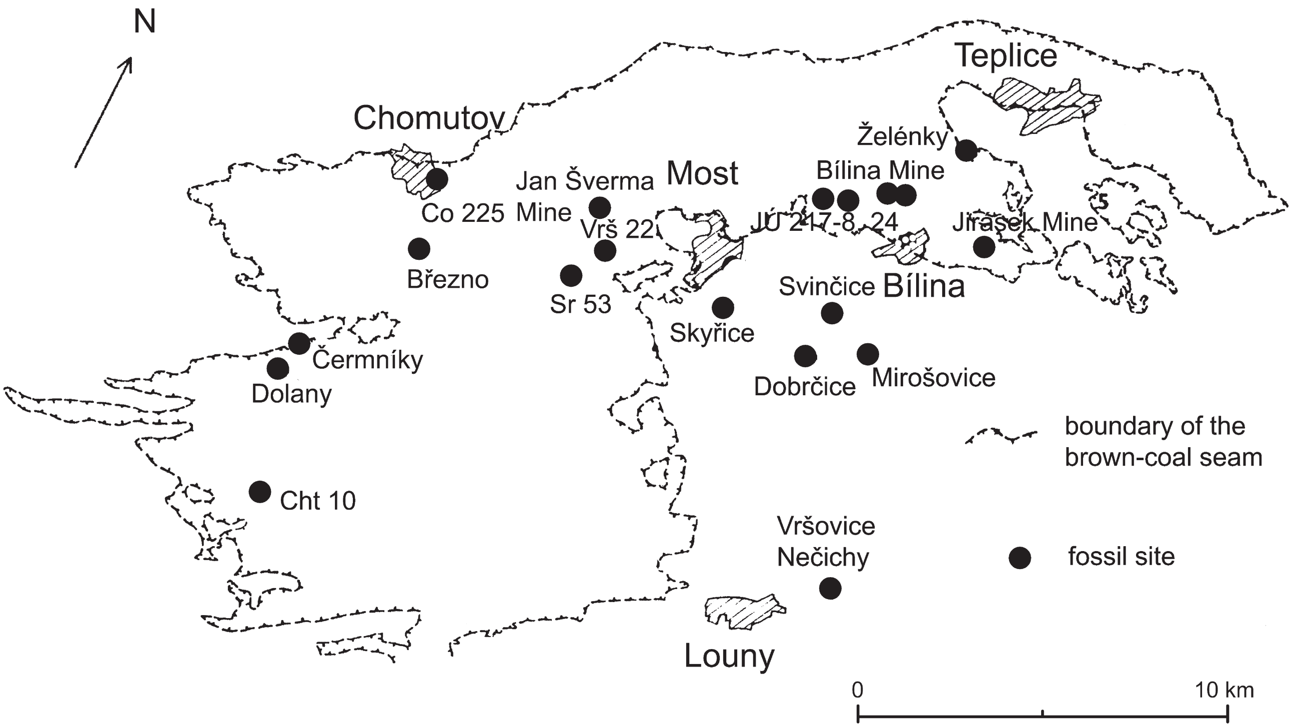

Fig. 1. Geographical position of the cited fossil localities in the Most Basin (see also Bůžek – Holý, 1964, Bůžek et al., 1992, Hurník – Kvaček, 2000).

The repositories, as far as known, are indicated in the systematic part below.

The photo-documentation has been prepared partly earlier by Mr. Skala working in the Geological Survey (most pictures of mesofossils), partly by the author (including type and original specimens from the 19th century).

Systematic part

Family Malvaceae Juss. s.l.
Subfamily Tilioideae Arn.

Genus *Craigia* W. W. Smith – Evans

Craigia bronnii (Unger) Kvaček – Bůžek – Manchester (fruits, flower buds, flower)

Figs 2–3

Synonymy of the records from the Most Basin

1837–1838 *Ulmus* (? *Europaea*); Bronn, p. 14 (explanations of atlas), pl. 35, fig. 12; p. 864, nom. inval. (? Commotau=Chomutov, missing).

1845–1847 *Ulmus bronnii* Unger, p. 100, pro parte, pl. 26, figs 2–4 (Bilin=Bílina, BP – including lectotype and paratypes).

1866 *Ulmus bronnii* Unger; Ettingshausen, p. 62, pro parte, pl. 18, figs 1–5 (Prisen=Břežánky, BP, BA).

1866 *Ulmus longifolia* Unger; Ettingshausen, p. 62, pro parte, pl. 18, fig. 8 (Prisen=Břežánky, missing).

1881 *Ulmus longifolia* Unger; Velenovský, p. 25, pro parte, pl. 3, figs 24–25 (Vršovic= Vršovice at Louny, NM).

1971 *Pteleaecarpum europaeum* (Bronn) Bůžek – Knobloch; Bůžek, p. 70, pl. 31, figs 1–21 (Čermníky, UUG).

1989 *Pteleaecarpum bronnii* (Unger) Weyland; Bůžek – Kvaček – Manchester, p. 484, pro parte, figs 3–6, 27 (Břešťany, Čermníky, Březno, NM, UUG).

1991 *Craigia bronnii* (Unger) Kvaček – Bůžek – Manchester, p. 522.

1999 *Craigia bronnii* (Unger) Kvaček – Bůžek – Manchester; Hurník – Kvaček, p. 653, fig. 5 (Skyřice, Marianna Mine, MM).

2000 *Craigia bronnii* (Unger) Kvaček – Bůžek – Manchester; Kvaček – Hurník, p. 13, pl. 5, fig. 11, text-fig. 1.12 (Želénky, Svinčice, Mirošovice, Vršovice and Nečichy at Louny, DB, NM).

2000 *Craigia bronnii* (Unger) Kvaček – Bůžek – Manchester; Sakala, p. 63, pl. 6, fig. 6 (Bílina Mine, DB).

2001 *Craigia bronnii* (Unger) Kvaček – Bůžek – Manchester; Hably – Erdei – Kvaček, p. 62, 75, pl. 84, figs 3–4, pl. 103, fig. 3, pl. 104, figs 2–3 (Bílina area, BP – including lectotype and paratypes).

2004a *Craigia bronnii* (Unger) Kvaček – Bůžek – Manchester; Kvaček et al., p. 120, fig. e (Bílina Mine, DB).

Lectotype selected here: BP 55.2308.1, Unger, 1845, pl. 26, fig. 2 – re-figured in Hably et al., 2001, pl. 103, fig. 3 and in this paper, Fig. 3.1 (Břešťany Clay, Bílina area).

Paratypes selected here: BP 55.2297.1, 55 2301.1, Unger, 1845, pl. 26, figs 4 left and right, re-figured in Hably et al., 2001, pl. 104, figs 2–3 and in this paper Figs 3.2–3 (Břešťany Clay, Bílina area).

Because the type specimens published by Unger (1845–1947) have been recovered by the author in the Hungarian Natural History Museum, Budapest, the neotype selected for *Pteleaecarpum bronnii* by Bůžek et al. (1989) must be replaced by a lectotype selected above.

Material: strongly compressed carbonised mesofossils isolated by sieving – more than 10 flower buds, 1 flower and more than 5 carpels and very young immature fruits, compressions of an immature fruit and a great number of isolated valves, partly closely grouped and with adhering seeds, impressions of a fruit and a great number of isolated valves, partly folded, occasionally two valves adhering together.

Description: Flower buds (Figs 2.1–4) broadly ellipsoidal to globular, rarely conical, 1.5–2 mm wide and 1.2–2.3 mm long, usually rugulose, attached to stout short stalks, demarcations of 5 tightly closed sepals visible as small ribs on the surface. Pollen in situ of the *Intratriporopllenites*-type. An undeveloped, permineralised (pyritised) flower (Fig. 2.12) ca. 5 mm wide and 2.5 mm high, laterally compressed, attached to a 4 mm long stout stalk, sepals widely open, rugulose on outer surface, crescent-shaped, ca. 2 mm long, probably 5 in number, inside the flower a few spindle-shaped bodies, probably remains of enveloped bundles of stamens. No other floral organs preserved. Immature fruits or carpels (Figs 2.5–10) ovoid to obovoid, 1.5–2 mm long and 1.2–2 mm in diameter, 5-angular to deeply winged, exceptionally attached to a short stalk, smooth on the surface. Compressions/impressions of small fruits (Figs 2.11, 3.4–5) 5–10 mm in diameter with longer stalks preserved, laterally strongly compressed, originally globose, with wings well compressed into coal matter, in the case of an impression with starting dehiscence of the wings, covering and overlapping each other. Detached valves (Figs 3.1–3) and groups of valves (Fig. 3.6) usually spreading, sub-orbicular to obovate, reaching a length of 24 mm, in the mean 17–18 mm in diameter, showing a prominent fusiform locular area divided by the medial suture. Remains of aborted seeds

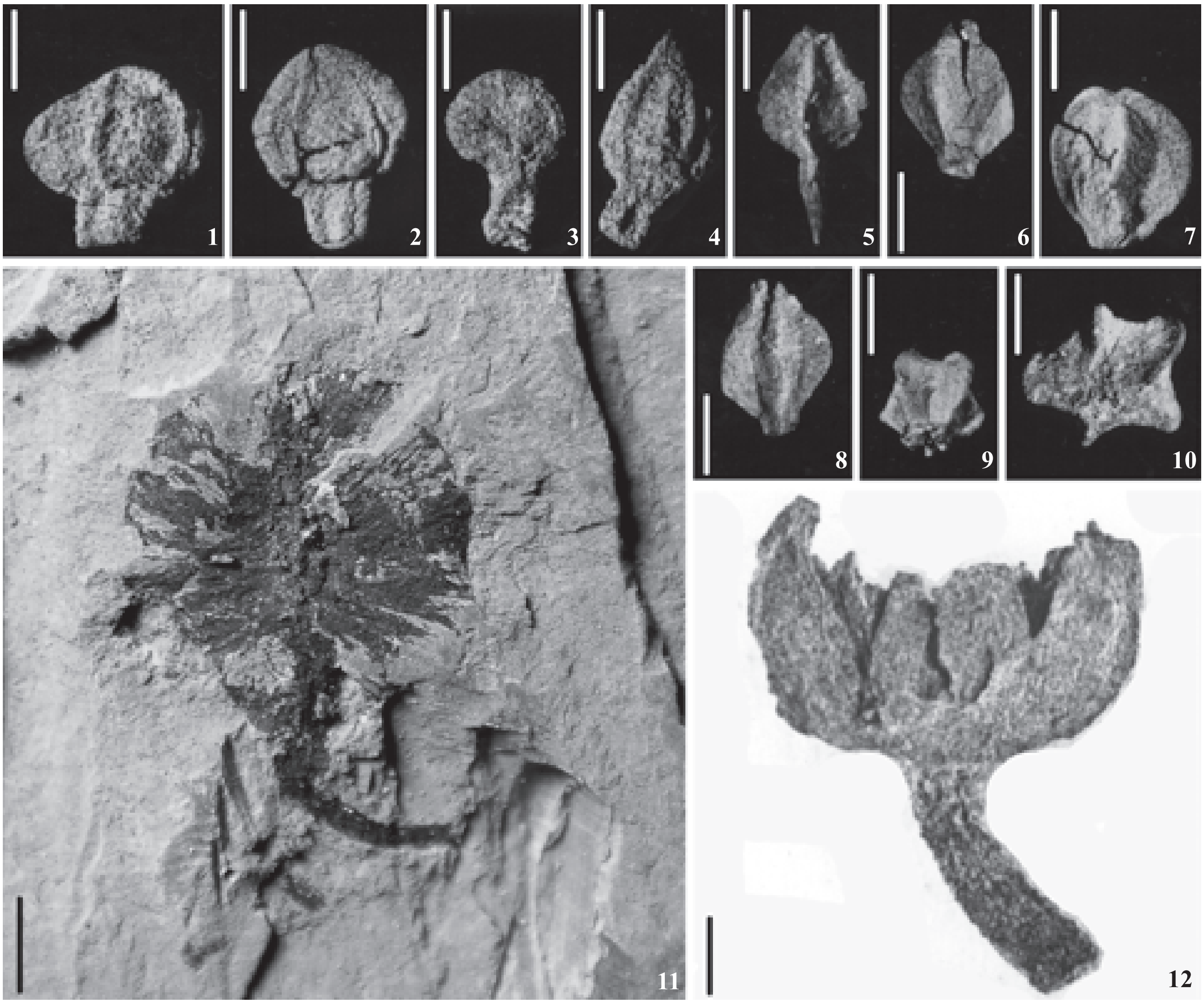

Fig. 2. 1–12 – *Craigia bronnii* (Unger) Kvaček – Bůžek – Manchester. 1–4 – four flower buds, 1 – specimen destroyed by maceration, core JÚ 218, depth 132.4 m, 2 – NM G 8469, core Sr 53, depth 55 m, 3 – NM G 8471, core Sr 53, depth 55 m, 4 – NM G 8463, core JÚ 218, depth 132.4 m, all scale bar = 1 mm, 5 – stalked immature fruit, NM G 8462, core JÚ 218, depth 132.4 m, scale bar = 1 mm, 6 – deeply ribbed detached carpel, lateral view, NM G 8464, core JÚ 224, depth 149.7 m, scale bar = 1 mm, 7 – flattened immature fruit, NM G 8467, core Cht 10, depth 10.33 m, scale bar = 1 mm, 8 – deeply ribbed detached carpel, NM G 8466, core Co 225, depth 57.8 m, scale bar = 1 mm, 9 – detached carpel shown in fig. 2.6 from below, scale bar = 1 mm, 10 – immature 5-winged fruit compressed from above, NM G 8461, core JÚ 218, depth 132.4 m, scale bar = 1 mm, 11 – shortly stalked undeveloped fruit showing fine radial venation of wings, NM G 8476, Bílina Mine, Horizon 30, scale bar = 2 mm, 12 – laterally compressed undeveloped flower with crescent-shaped sepals and spindle-shaped bodies inside, NM G 8465, core Sr 53, depth 55 m, scale bar = 1 mm.

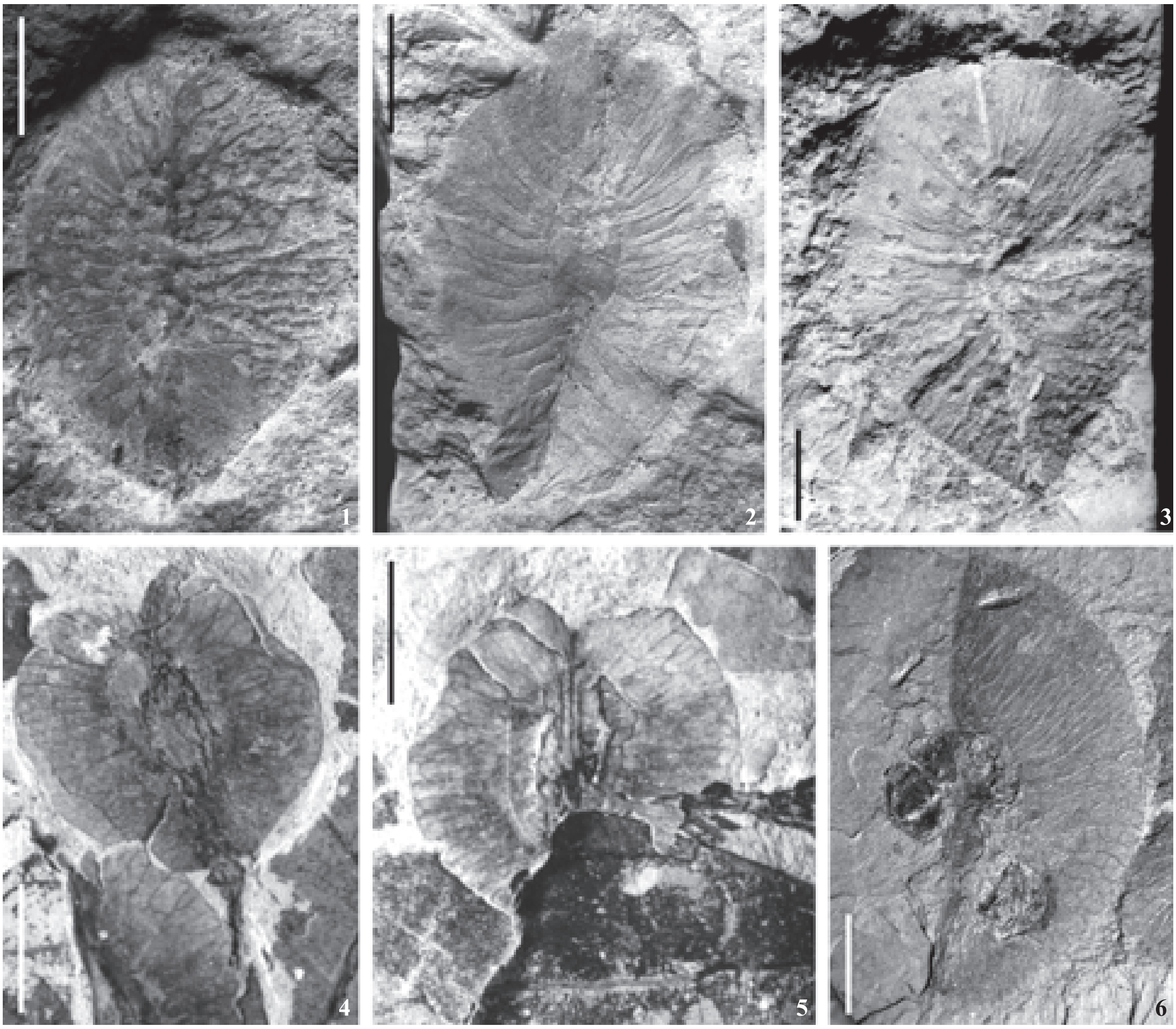

Fig. 3. 1–6 – *Craigia bronnii* (Unger) Kvaček – Bůžek – Manchester. 1 – lectotype (Unger, 1845–1847, pl. 26, fig. 2), BP 55.2308.1, Břežánky, scale bar = 5 mm, 2 – paratype, (Unger, 1845–7, pl. 26, fig. 4 left), BP 55.2297.1, Břežánky, scale bar = 5 mm, 3 – paratype, (Unger, 1845–1847, pl. 26, fig. 4 right), BP 55.2301.1, Břežánky, scale bar = 5 mm, 4 – a young fruit on the stalk thickened in its upper part with scars of sepals, NM G 8474a, Bílina Mine, Horizon 24, scale bar = 5 mm, 5 – counter-impression of fig. 3.4 showing margins of several overlapping dehiscing valves, NM G 8474b, Bílina Mine, Horizon 24, scale bar = 5 mm, 6 – a back-folded valve with attached and slightly dislocated seeds, NM G 8475, Bílina Mine, Horizon 30, scale bar = 5 mm.

biserial, attached to the suture, mature seeds (Fig. 3.6) attached or dispersed nearby the valves, dark carbonised, ca. 3 mm long, not showing details of the hilum and surface structure. Venation of the valves reticulate, in radial rows, typically steeper in the apical part. Multiradial trichomes on the outer surface of the valves (see also description in Bůžek et al., 1989).

Discussion: Similar flower buds and immature detached fruits/carpels along with mature capsules have been recovered by Pingen (Pingen et al., 2001) in the Hambach Mine, Lower Rhine Embayment, in much better state of preservation. The same layers yielded also leaves of *Dombeyopsis lobata* (coll. Utrecht Univ., author's observation). The sieved specimens from the Most Basin are smaller, partly strongly pyritised and not connected with transitions to ripe fruits. This may be due to rough sieving technique, which damaged delicate winged capsules. Very similar, but also slightly larger fossils with tilioid pollen in situ and identical in shape and sculpture have been described from Saxony as *Burretia insculpta* (Mai, 2000). The identity with the Czech material is highly probable, although fruits of *Craigia bronnii* are unknown from these deposits at Brandis, only accumulations of *Dombeyopsis lobata* foliage in coal facies (Mai – Walther, 1991). The fruit valves from the Most Basin are among the largest in Europe, competing in the size with those from Rott (Weyland, 1948), although variation in the size occurs; like in the extant *Craigia yunnanensis* (Kvaček et al., 2002). The mean size cannot be easily applied for discrimination of small taxonomic entities, even during the whole geological history of *Craigia*, while differences in associated foliage may help in this respect (Kvaček – Akhmetiev – Manchester in prep.). The morphological and anatomical structure of the fruits remains very conservative and survives almost unchanged to the present except subtle differences, e.g. in the position of the hilum (Kvaček et al., 2002).

Occurrence: mesofossils of flower buds and immature fruits – Bílina area, cores Jenišův Újezd JÚ 217, depth 72.6, 132.7 m, JÚ 218, depth 132.4–5 m, JÚ 224, depth 149.7 m, Žatec–Chomutov area, cores Chomutov, Co 225, 57.8 m, Chotěbudice, cores Cht 10, depth 33 m, Strupčice, Sr 53, depth 55 m, Vršany, Vrš 22, depth 79–80 m, Most area, Jan Šverma Mine; fruits and detached valves – Bílina–Duchcov area, Břešťany, Břežánky, Jenišův Újezd, former Maxim Gorkij Mine, now Bílina Mine, Želénky–Zabrušany, Svinčice, Mirošovice; Louny area, Vršovice, Nečichy; Most area, Skyřice; Žatec–Chomutov area, Čermníky, Březno, ?Chomutov.

Morpho-genus: *Dombeyopsis* Unger

Dombeyopsis lobata Unger (foliage)
Fig. 4

Synonymy of the records from the Most Basin
1850a *Dombeyopsis lobata* Unger, p. 447 (Bilin=Bílina, BP).
1850a *Dombeyopsis grandifolia* Unger, p. 447, pro parte (Bilin=Bílina, non Prevali, Kainberg, Leoben, ? BP).
1850a *Dombeyopsis sidaefolia* Unger, p. 448. (Bilin=Bílina, BP).
1850a *Dombeyopsis tiliaefolia* (A. Braun) Unger, p. 447, pro parte (Bilin=Bílina, non Oehningen, coll. ?).
1850b *Dombeyopsis tiliaefolia* (A. Braun) Unger; Unger, p. 174, pro parte, pl. 25, fig. 3 (non figs 1–2, 4) (Bilin=Bílina, missing).
1850b *Dombeyopsis grandifolia* Unger; Unger, p. 175, pro parte, pl. 27, fig. 2 (non fig. 1 nec pl. 26) (Bilin=Bílina, missing).
1860 *Ficus tiliaefolia* (A. Braun) Heer; Unger, p. 14, pl. 6, fig. 2 (Bilin=Bílina – type of *Dombeyopsis sidaefolia* Unger, BP).
1860 *Ficus dombeyopsis* Unger, p. 13, pl. 5, figs 1–5, pl. 6. fig. 1, nom. illegit. superfl. (Salzhausen, Bilin=Bílina, pl. 6, fig. 1 type of *Dombeyopsis lobata* Unger, BP, partly missing).
1866 *Cecropia europaea* Ettingshausen, p. 82, pl. 28, figs 1–2 (Priesen=Břežánky, missing).
1866 *Cecropia heerii* Ettingshausen, p. 82, pl. 27, pl. 28, fig. 7 (Priesen=Břežánky, BP).
1866 *Ficus tiliaefolia* (A. Braun) Heer; Ettingshausen, p. 80, pl. 25, figs 4, 5, 7, 10 (lectotype) (Preschen= Břešťany, Priesen=Břežánky, Sobrussan=Zabrušany, BP, BA).
1874 *Sterculia dombeyopsis* (Unger) Schimper, p. 102.
1881 *Ficus tiliaefolia* (A. Braun) Heer; Velenovský, p. 28, pl. 6, figs 1–4 (Vršovic=Vršovice at Louny, NM).
1891 *Ficus tiliaefolia* (A. Braun) Heer; Engelhardt, p. 162, pl. 9, fig. 25, pl. 10, fig. 9 (Schellenken=Želénky, missing).
1965 *Dombeyopsis lobata* Unger; Knobloch – Kvaček, p. 134, text-fig. 10 (Želénky, missing).
1971 *Dombeyopsis lobata* Unger; Bůžek, p. 70 (Čermníky, Dolany, UUG).
1999 *Dombeyopsis lobata* Unger; Hurník – Kvaček, p. 653, pl. 4, figs 2–3 (Skyřice, MM).
2000 *Dombeyopsis lobata* Unger; Kvaček – Hurník, p. 13, pl. 5, fig. 12, text-figs 1.17, 3.7 (Vršovice at Louny, Želénky, Jirásek Mine, Dobrčice, Svinčice, Dolany, DB, NM, MM, partly missing).
2000 *Dombeyopsis lobata* Unger; Sakala, p. 62, pl. 6, fig. 5 (Bílina Mine, DB).
2001 *Dombeyopsis lobata* Unger; Hably – Erdei – Kvaček, p. 77–78, pl. 67, fig. 1, pl. 90, fig. 2 (Bílina area, BP – lectotype).
2004a *Dombeyopsis lobata* Unger; Kvaček et al., p. 120, fig. d (Bílina Mine, DB).

Lectotype selected here: BP 59.686.1, Unger, 1850a, p. 447, figured as *Ficus dombeyopsis* Unger, 1860, pl. 6, fig. 1; refigured as *Ficus tiliaefolia* sensu Ettingshausen, 1866, pl. 25, fig. 10 and in Hably et al., 2001, pl. 67, fig. 1 and pl. 110, fig. 1, in the present paper Fig. 4.1 (Břesťany Clay, Bílina area).

Material: compressions and impressions of complete leaves and fragments, cuticle preparations.

Description: Leaves simple, long petiolate, petiole thick, usually attaining half to full length of the lamina, attached from the underside of the lamina, lamina circular to broadly oval, unlobed (Fig. 4.2) to shallowly trilobate (Figs 4.1, 3 and 4), ca. 35 to 300 mm in diameter, margin entire to wavy to fine dentate (dentate forms more frequent in drier habitats outside the Most Basin, e.g. in the Oligocene of Bechlejovice), base symmetrical, shallowly to deeply cordate, apex and lobes wide triangular, blunt, rarely acuminate or apiculate, texture thin. Venation palmate, 5 to 7 primaries radiating from the base, giving off very regular and curved secondaries on either side on the mid-vein and lateral primaries; three inner primaries reaching lobes, secondaries often also on either side of the lateral primaries partly forked near the margin, tertiaries percurrent or once forked, dense, arranged in a spider net manner between the primaries, and perpendicularly to the secondaries, higher order venation regularly reticulate. Cuticles thin, lamina chartaceous. Stomata anomocytic, glandular trichomes barrel-shaped, composed of more cells arranged in equatorially oriented segments, non-glandular trichomes rarely simple, much more frequently fasciculate to stellate, with (2–) 4–6 (rarely more) rays, those on veins fasciculate, with stronger rays up to 300 mm long, in intercostals areas thin-walled, adpressed, with ca. 75 mm long rays, rarely preserved.

Discussion: This type of peculiar large foliage has been reported under various names from nearly all sites of Europe, where *Craigia* fruits occur. The type locality of both *Craigia bronnii* and *Dombeyopsis lobata* is Bílina, namely the clay-pits for ceramic clay (called Břešťany Clay) formerly situated between Bílina and villages Břešťany, Břežánky and Jenišův Újezd (today removed by mining). The above characteristic, particularly the cuticular structure, is mainly based on the topotypical specimens from the new exposures in the Bílina Mine (Sakala, 2000, Kvaček – Worobiec – Worobiec in prep.). The newly obtained cuticles correspond in the structure with those described in detail in Knobloch – Kvaček (1976) and Walther (in Mai – Walther, 1991). The variation in shape of the lamina, which is simple to mostly trilobate, but symmetrical, is not so great as the variation in size from small to extremely large leaves (Figs 4.3–4), and particularly in the character of the margin. As noted at several occasions (Knobloch – Kvaček, 1976, Knobloch, 1998), the margin can be entire, wavy, but also very distinctly simple dentate. Such transitions occur particularly in the sites outside brown-coal basins, e.g., in the Early Oligocene diatomite of Bechlejovice (Kvaček – Walther, 2004) or the Pliocene maar-fill of Willershausen (Knobloch, 1998). The leaf forms without lobes,

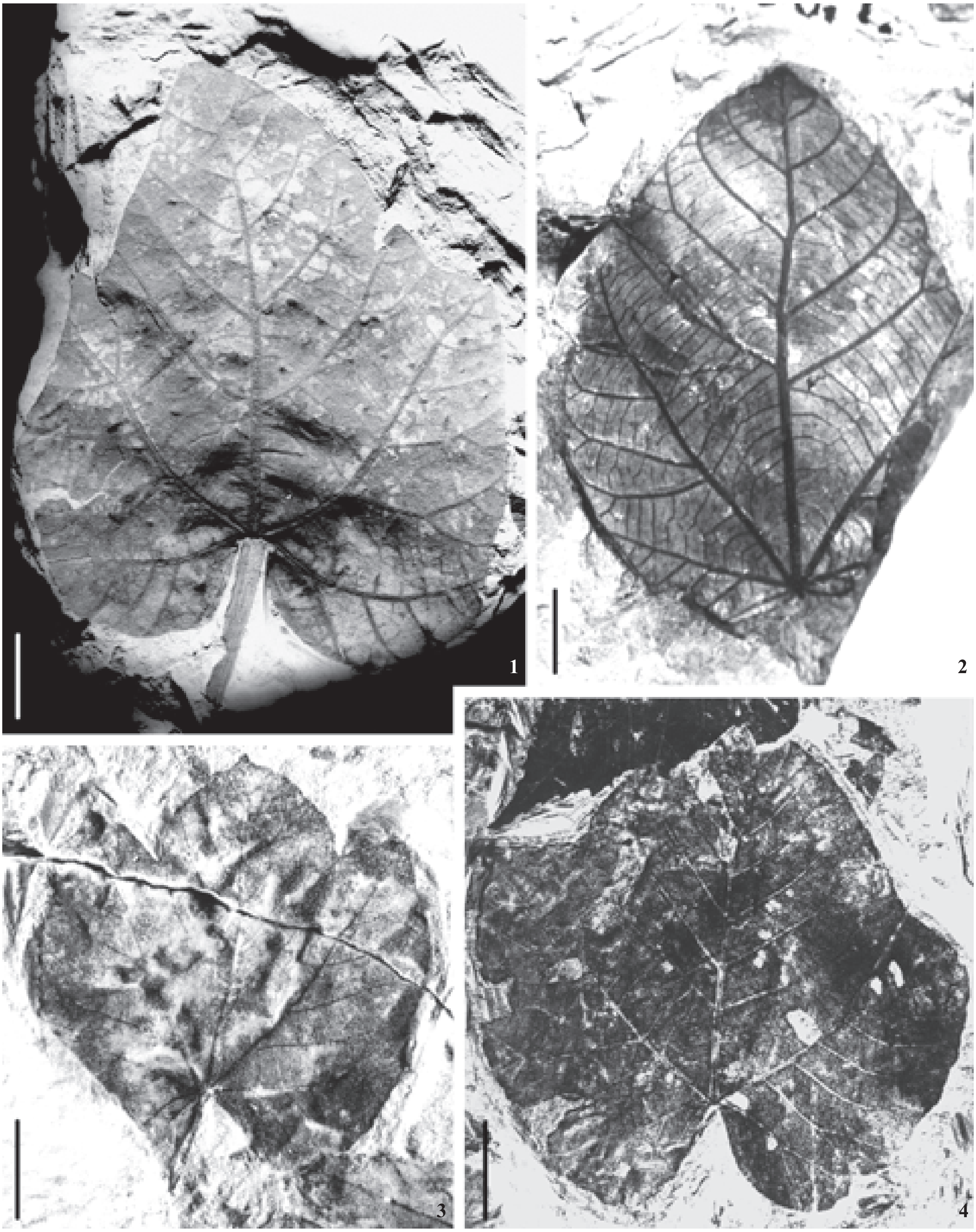

Fig. 4. 1–4 – *Dombeyopsis lobata* Unger. 1 – lectotype (Unger, 1860, pl. 6, fig. 1, as *Ficus dombeyopsis* Unger), BP 59.686.1, Břežánky, scale bar = 10 mm, 2 – type of *Dombeyopsis sidaefolia* Unger (Unger, 1860, pl. 6, fig. 2, as *Ficus tiliaefolia* (A. Braun) Heer), BP 64.300.1, Břežánky, scale bar = 10 mm, 3 – extremely small leaf, UUG Če 155a-1015, Čermníky, scale bar = 10 mm, 4 – larger leaf, UUG Če 155a-1014, Čermníky, scale bar = 20 mm.

which were assigned originally to *Dombeyopsis sidaefolia* Unger and *Ficus tiliaefolia* auct. [non (A. Braun) Heer], recall two other leaf taxa known from European Tertiary. The first one, *"Ficus" truncata* Heer, differs by thinner and less regular venation, but coincides in the shape of the lamina, which is also symmetrical, the base varies from cuneate to truncate (rarely to cordate). The apex is usually elongate and strikingly narrowed and acuminate (Bůžek, 1971). There are also subtle differences in epidermal structure (Kvaček – Worobiec – Worobiec in prep.). The second morpho-species, *Byttneriophyllum tiliaefolium* (A. Braun) Knobloch – Kvaček, formerly known as *Ficus tiliaefolia* (A. Braun) Heer and often misidentified with *Dombeyopsis lobata*, differs in strongly asymmetrical leaf base (Knobloch – Kvaček, 1965). This leaf morpho-type is in Europe and rarely in East Asia associated with the fruits of "giant maple" *Banisteriaecarpum giganteum* (Goeppert) Kräusel and occurs only later in the Miocene to Pliocene, not in the Most Basin.

The views on the affinities of *Dombeyopsis lobata* have changed since the first description by Unger (1850a) was published. He was in fact near the truth comparing it with foliage of *Dombeya* of the Malvaceae, Dombeyoideae. Later on, under the influence of Heer, he rejected this idea and turned to the Moraceae. At this occasion he renamed it into *Ficus dombeyopsis* Unger, nom. illegit. superfl. (Unger, 1860). This idea was later followed by Ettingshausen (1866), who misinterpreted *Dombeyopsis lobata* for *Ficus tiliaefolia* (A. Braun) Heer (= *Byttneriophyllum tiliaefolium* (A. Braun) Knobloch – Kvaček) and maintained it as a representative of *Ficus* (Moraceae). Besides, he assigned its extremely large leaves to *Cecropia* of the same family. According to a large size and shape of leaves, Laurent (1904–1905) believed to find in this foliage type a new fossil *Paulownia*. The most other palaeobotanists returned to the original interpretation and matched (recombined) *Dombeyopsis lobata* with *Sterculia*, *Firmiana*, or *Bombax* of the Malvales (for the review see Knobloch, 1969).

The cuticular structure proves the affinity to Malvales. The combination of fasciculate to stellate and glandular barrel-shaped trichomes is typical of many malvalean genera (e.g. *Hainania*, *Tilia*, *Colona*, *Brownlowia*, and also *Craigia*). However, the generic distinction is difficult on the basis of epidermal anatomy due to uniform structural traits and their variation within one genus. *Craigia yunnanensis* does not deviate from this general type of epidermal structure. However, stellate to fasciculate trichomes are only on veins, while scattered simple and paired trichomes prevail in intercostals areas; leaves of the population from Tonkin are hairless (Kvaček – Worobiec – Worobiec in prep.). Only by a regular association of *Dombeyopsis lobata* with *Cragia* fruits we can assume that this is the foliage of the same plant. The extant species of *Craigia* differ in mostly truncate (*Craigia yunnanesis*) to narrow cuneate leaf basis (*Craigia kwangsiensis*) and always non-lobed ovate lamina. There is a variation in leaf margin from distinctly to indistinctly simple dentate (most populations of *C. yunnanesis*) to sub-entire (*C. yunnanensis* from Tonkin – Fig. 5). The latter, which is the southernmost population of this species, has also slightly cordate leaves and matches best simple leaf forms of *Dombeyopsis lobata*. The petiole is also quite long in comparison with the lamina, like in *Dombeyopsis lobata*.

Occurrence in the Most Basin: Bílina–Duchcov area, Břešťany, Břežánky, Jenišův Újezd, former Jirásek Mine, former Maxim Gorkij Mine, now Bílina Mine, Želénky–Zabrušany, Svinčice, Dobrčice; Louny area, Vršovice, Nečichy; Most area, Skyřice; Žatec–Chomutov area, Čermníky, Dolany.

***Craigia bronnii* & *Dombeyopsis lobata* whole plant concept**

Fig. 6

Like the taxonomic position of the *Craigia* fruits, the associated leaves remained long time misinterpreted, all previous authors, even meeting them on the same spot, never thought that they might have come from the same plant. Unger (1850a) first recognised malvalean affinities of the foliage but was in error, when he identified the fruits with *Ulmus*. Laurent (1904–1905) studying another concentration of *Craigia* in the Late Miocene volcanoclastics at La Mougudo, Cantal, was sure that the fruits belonged to *Abronia*, and assigned the abundantly co-occurring leaves to *Paulownia*. Bůžek et al. (1989) interpreted the fruits as 3-winged capsules of Sapindaceae and did not suggest any associated foliage that would fit in this concept. Only after the malvalean affinities of the fruits were recognised it has become clear that *Dombeyopsis lobata* is the best candidate, at least for the European populations, to be combined into the whole plant of *Craigia bronnii* as a morpho-taxon of leaves (Kvaček, 1993). Now the European sites of *Craigia* fruits numbering over 70 (Kvaček – Akhmetiev – Manchester in prep.) yielded in 80% cases also leaves of *Dombyeopsis lobata.* The same phenomenon is clearly seen in the Most Basin, where fruits and leaves of this plant are usually bound to coal facies, i.e. in parautochthonous assemblages, where no other tilioid leaves co-occur. It is true that abundance of the two organs may vary from site to site and there are cases that sometimes one or the other is absent. This is, of course, valid for other deciduous trees as well, for which the combination of fruits and leaves is well apparent – maple, elm, alder, or birch. Taphonomic processes and various time of ripening/leaf shedding are surely responsible for these irregularities. Large leaves of *Dombeyopsis lobata* were usually not transported for long distances while wind-dispersed valves of *Craigia* could easily reach depositional sites far from the tree. It is particularly the case of allochthonous delta deposits in the Bílina area (higher fossiliferous horizons in the Bílina Mine), where fruit valves are common, but they

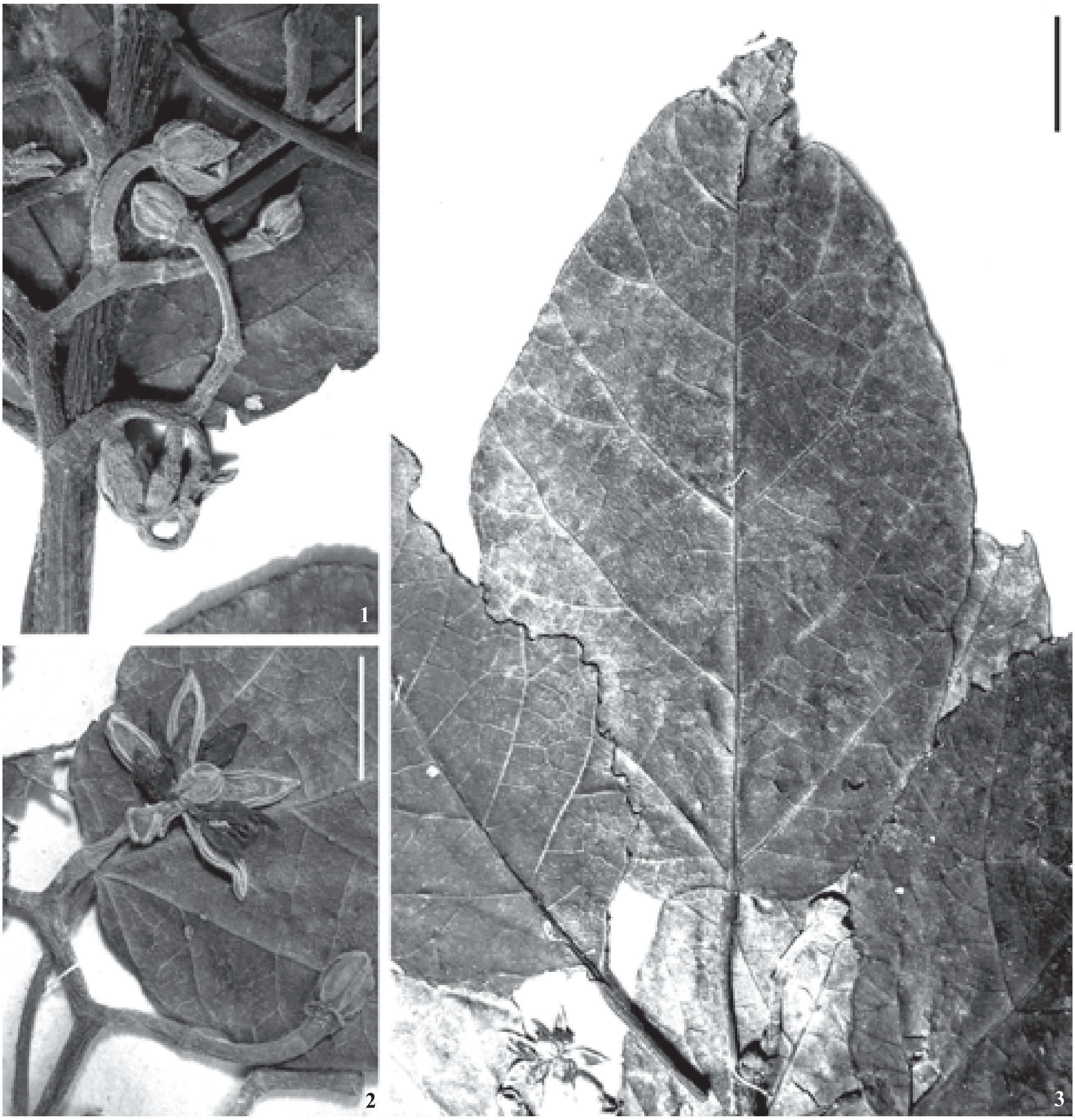

Fig. 5. 1–3 – *Craigia yunnanensis* W. W. Smith – Evans, *Pételot 3810,* Herb. Paris, Tonkin. 1 – flower buds and immature flowers & carpels, scale bar = 10 mm; 2 – flower showing calyx, five groups of enveloped stamens and a carpel, scale bar = 10 mm; 3 – twig with long petiolate, entire-margined leaves, scale bar = 20 mm.

are rarely accompanied with *Dombeyopsis lobata*. The accumulation of leaves in coal swamp settings is a good argument that *Craigia* was, at least within the Most Basin, a member of Early Miocene swamp forests close to well-inundated mires. The other populations outside Europe are mostly not of this kind. The *Craigia* fruits in the Tertiary of East Asia and western North America are accompanied with strongly asymmetric foliage of the *Plafkeria* type and obviously belong to a different species (Kvaček – Akhmetiev – Manchester in prep.). In this respect, Bůžek et al. (1989) were wrong to include into their concept of *Pteleaecarpum bronnii* also all records from East and Central Asia. It is also the reason, why the foliage should be maintained in separate morpho-taxa.

The flower buds known only from Europe have yielded pollen of the *Intratriporopollenites*-type. Zetter (in Kvaček et al., 2002) showed a great similarity between the fossil pollen obtained from flower buds of *Craigia bronnii* and that of *Craigia yunnanensis* and arrived to a conclusion that SEM studies are necessary for safe identifications of such pollen morpho-types. As most of the fossil pollen taxa have not been revised in this respect,

Fig. 6. Reconstruction of the *Craigia bronnii* & *Dombeyopsis lobata* plant according to co-occurrence of fruits and leaves in the Most Basin, scale bar = 20 mm.

it is difficult to decide what morpho-taxon of dispersed pollen belongs to *Craigia bronnii.* As stressed by Krutzsch (2004), the *Craigia* type of pollen is mostly concentrated in the Late Eocene deposits of Europe, which is in strong discrepancy with the occurrence of the fruits. However, the tilioid type of pollen is well represented in the Malvaceae s.l. and transitions between the genera or even variation within a genus and species (Krutzsch, 2004, Zetter's observation in *Craigia yunnanensis*) may thwart attempts of a very precise splitting of this pollen group. The most common morpho-taxon of dispersed pollen, which is identified in connection with *Craigia bronnii* is *Intratriporopollenites insculptus* (i.e. *Burretia insculpta*), which is typified by the specimens from Brandis and Altmittweida in Saxony, i.e. from the deposits equivalent to the Most Formation (Mai, 1961, Mai – Walther, 1991). The flower buds with the same pollen (Mai, 2000) are very similar to those from the Most Basin described above. A separate study is being prepared (Kvaček – Worobiec – Worobiec) devoted to the dispersed and in situ pollen, accompanying the *Craigia* megafossils in the Most Basin and elsewhere. Accumulations of *Intratriporopollenites insculptus* were described from various horizons of the Main Coal Seam in the Most Basin (Konzalová, 1976).

Associated vegetation and autecology

In the flora of the Most Formation almost 200 plant species based on mega- and mesofossils have been recognised and recorded to date. *Craigia* records are all concentrated in the middle part of the formation. Two depositional centres, called the Žatec and Bílina deltas, were two major sources of plant fossils and represent lateral equivalents of the brown coal deposits, i.e. the Holešice Member, and the lowermost levels (Břešťany Clay) of the Libkovice Member. The floras of both areas contain *Craigia*. They are very similar to each other, the former having more frequent ferns (*Woodwardia*, *Pronephrium* – Bůžek, 1971), the latter including more thermophile elements, particularly sabaloid and calamoid palms (Kvaček et al., 2004b). The index fossil *Schenkiella credneri* (syn. *"Trapa" credneri*), which occurs in the Bílina area, suggests a direct correlation with the

Brandis flora (Third Lusatia Coal Seam) in Saxony (see Mai – Walther, 1991, Kvaček et al., 2004b).

The regular association of *Craigia bronnii* & *Dombeyopsis lobata* plant with *Taxodium*, *Quasisequoia*, *Glyptostrobus* and a number of deciduous broad-leaved trees and other plants of moist habitats, e.g. *Alnus*, *Nyssa*, *Acer tricuspidatum, Fraxinus, Decodon,* leads to a conclusion that *Craigia* thrived at that time on emergent mineral periphery of deep peat swamps (Kvaček, 1998). Mach (in Kvaček et al., 2004a, b) characterised such stands as wetland forest vegetation in back swamp along streams and in deltas on clayey and silt fat soils with an irregular supply of nutrients and the groundwater level near or above the earth surface. This vegetation type corresponds to the *Taxodium-Nyssa* association *sensu* Bůžek – Kvaček (in Boulter et al., 1993). The mixture of the above-mentioned swamp vegetation with other deciduous (Ulmaceae, Betulaceae, *Comptonia*, *Parrotia*, *Podocarpium*) and evergreen elements (*Quercus rhenana*, *Myrica lignitum*, Lauraceae, *Trigonobalanopsis*) as well as frequent pine fossils is typical of the Břešťany Clay, the type horizon of *Craigia bronnii* and also *Dombeyopsis lobata.* Palaeoclimatic conditions can be estimated as humid subtropical to warm-temperate, with the mean annual temperature about 13–16°C and with the coldest month mean above 0°C (Kvaček et al., 2004b). Thus in all occurrences within the Most Formation, the fossil *Craigia* slightly differs from its living relative *Craigia yunnanensis* in autecology. Extant stations of the latter fall into the paratropical to subtropical zones of SE Asia within upland notophyllous forests dominated by evergreen Fagaceae or thickets in valleys between 1000 to 2700 m alt. Only rarely, *Craigia* entered forests in southern China with more extensive representation of deciduous arboreal elements and was never found in the present vegetation in lowland swamps (e.g., in relictual stands of *Glyptostrobus* in the Zhu Jiang delta in Guangdong). We may speculate that the European Tertiary populations of *Craigia* found niches in the landscape more suitable for deciduous arboreal elements, after having arrived from high latitudes during the Palaeogene to Central Europe from the ancient Arctic deciduous forests. As comparative studies of the nearest living relatives progress, similar cases of such Tertiary relics have been found, which possibly changed autecology during the Cenozoic (Kvaček submitted).

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Spodnomiocenní doklady rodu *Craigia* (Malvaceae s.l.) v mostecké pánvi v severních Čechách – celostní přístup

Mostecká pánev je místem největší koncentrace fosilních nálezů reliktního rodu *Craigia*, dnes přežívajícího jen na několika místech v jižní Číně a severním Vietnamu. Také odtud byl poprvé popsán druh *Craigia bronnii* (jako *Ulmus bronnii*) založený na plodních zbytcích podobných jilmovým nažkám. Tato konvergence i s řadou jiných křídlatých plodů vedla v minulosti k mnoha mylným systematickým interpretacím. Po objevení celých plodů – pětikřídlých tobolek a souběžných nálezů květních poupat není dnes pochyb o jejich příslušnosti k zmíněnému reliktnímu rodu z čeledi Malvaceae, podčeledi Tilioideae. Časté souběžné výskyty listů, řazených k morfologické jednotce *Dombeyopsis lobata*, dovolují dnes charackterizovat celou tuto fosilní rostlinu včetně detailů květů, objevených v mostecké pánvi a pylu. Spodnomiocenní evropský zástupce rodu *Craigia*, alespoň podle nahromadění jeho fosilních zbytků v uhelné facii, byl strom snášející bažinné prostředí spíše opadavých porostů vroubících uhlotvorné močály. Tím se výrazně odlišoval od dnešního nejblíže příbuzného žijícího zástupce, *Craigia yunnanensis*, přežívajícího v horách jižní Číny a severního Vietnamu v sušších podmínkách paratropického až subtropického klimatu v lesích složených převážně ze vždyzelených zástupců bukovitých.