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

Spodnomicenní doklady rodu * Craiga * (Malvaceae s.l.) v mostecké pánvi v severních Čechách – celestní přístup

(6 figs)

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Fossil records of * Craiga bromii* (Malvaceae, Tilioidae) 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 synonyms are provided. The reconstructed plant is compared with the nearest living relative *Craiga 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 * Craiga * (Malvaceae s.l.). Its fruits have been long known from the European Tertiary and misidentified with various genera and families (e.g., * Ulmus*, * Abronia*, * Ruta*ceae, *Zygaephyllaceae* etc.). A wider comparative study resulted in assigning these very characteristic fossils to the genus * Craiga* (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 C. 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 * Craiga bromii*, as earlier recognised for the same kind of mesofossils in the Rhenish Miocene (Pingen et al., 2001). * Craiga* 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 * Craiga* 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 micropaleontological 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 * Craiga bromii*, and associated leaf remains of *Dombeyopsis lobata*, are partlycoalified compressions allowing preparation of cuticles, which come mostly from the Bílina Mine (see Bůžek et al., 1989 – as * Pteleaeacarpum*, 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 * Craiga* 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 Libkovic 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 Tuch enforce (MN 3b) indicate (for details of stratigraphy see Kvaček et al., 2004b).

New collections from the environs of Bílina were gathered by the late Čestmir Bůžek, recently by Zdeněk Dvořák, the author, and their co-workers and friends. This material is mostly housed in the Bílina Mine Headquart- ers, 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.
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 bronni (Unger) Kvaček – Bůžek – Manchester (flowers, 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 bronni Unger, p. 100, pro parte, pl. 26, figs 2–4 (Bilina=Binila, BP – including lectotype and paratypes).
1866 Ulmus bronni Unger; Ettingshausen, p. 62, pro parte, pl. 2, figs 1–5 (Prizen=Březánky, BP, BA).
1866 Ulmus longifolia Unger; Ettingshausen, p. 62, pro parte, pl. 18, fig. 8 (Prizen=Březánky, missing).
1881 Ulmus longifolia Unger; Velenovský, p. 25, pro parte, pl. 3, figs 24–25 (Vršovice= Vršovice at Louny, NM).
1971 Pteleacarpum europeum (Brom) Bůžek – Knobloch; Bůžek, p. 70, pl. 31, figs 1–21 (Čermníky, UUG).
1989 Pteleacarpum bronni (Unger) Weyland; Bůžek – Kvaček – Manchester, p. 484, pro parte, figs 3–6, 27 (Břešťany, Čermníky, Březno, NM, UUG).

1999 Craigia bronni (Unger) Kvaček – Bůžek – Manchester; Hurník – Kvaček, p. 653, fig. 5 (Škýřice, Marianna Mine, MM).
2000 Craigia bronni (Unger) Kvaček – Bůžek – Manchester; Kvaček – Hurník, p. 13, pl. 5, fig. 11, text-fig. 1.12 (Zelenky, Svinice, Mirošovice, Vršovice and Nečichy at Louny, DB, NM).
2000 Craigia bronni (Unger) Kvaček – Bůžek – Manchester; Sakala, p. 63, pl. 6, fig. 6 (Bilina Mine, DB).
2001 Craigia bronni (Unger) Kvaček – Bůžek – Manchester; Hably – Erdei – Kvaček, p. 62, 75, pl. 84, figs 3–4, pl. 103, fig. 3, pl. 104, figs 2–3 (Bilina area, BP – including lectotype and paratypes).
2004a Craigia bronni (Unger) Kvaček – Bůžek – Manchester; Kvaček et al., p. 120, fig. e (Bilina 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, Bilina 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, Bilina 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 Pteleacarpum bronni 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 *Intratriporopollenites*-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 remain 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
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 Dombyopsis 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 Craiga bronii are unknown from these deposits at Brandis, only accumulations of Dombyopsis 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 Craiga 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 Craiga, 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 – Bilina area, cores Jenišív 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, Chotěbuďice, cores Cht 10, depth 33 m, Strupčice, Sr 53, depth 55 m, Všany, Vš 22, depth 79–80 m, Most area, Jan Šverma Mine; fruits and detached valves – Bilina–Duchcov area, Bréšťany, Bréšťanksý, Jenišív Újezd, former Maxim Gorkij Mine, now Bilina Mine, Želněnky–Zabrušany, Svinčice, Mirošovice, Louny area, Všovice, Nečichy; Most area, Škyřice; Žatec–Chomutov area, Čermná, Brézno, ?Chomutov.

Morpho-genus: Dombyopsis Unger

Dombyopsis lobata Unger (foliage)

Fig. 4

Synonymy of the records from the Most Basin

1850a Dombyopsis lobata Unger, p. 447 (Bilín–Bilina, BP).

1850a Dombyopsis grandifolia Unger, p. 447, pro parte (Bilín–Bilina, non Prevali, Kámbík, Loeben, ? BP).

1850a Dombyopsis tiliaefolia Unger, p. 448 (Bilín–Bilina, BP).

1850a Dombyopsis tiliaefolia (A. Braun) Unger, p. 447, pro parte (Bilín–Bilina, non Oehminger, coll. ?).

1850b Dombyopsis tiliaefolia (A. Braun) Unger, p. 174, pro parte, pl. 25, fig. 3 (non figs 1–2, 4) (Bilín–Bilina, missing).

1850b Dombyopsis grandifolia Unger, p. 175, pro parte, pl. 27, fig. 2 (non fig. 1 nec pl. 26) (Bilín–Bilina, missing).

1860 Ficus tiliaefolia (A. Braun) Heer; Unger, p. 14, pl. 6, fig. 2 (Bilín–Bilina – type of Dombyopsis tiliaefolia Unger, BP).

1860 Dombyopsis lobata Unger, p. 13, pl. 5, figs 1–5, pl. 6, fig. 1, nom. illegit. superfl. (Salzhausen, Bilín–Bilina, pl. 6, fig. 1 type of Dombyopsis lobata Unger, BP, partly missing).

1866 Cecropia europea Ettingshausen, p. 82, pl. 28, figs 1–2 (Priesen–Bréšťany, missing).

1866 Cecropia heerii Ettingshausen, p. 82, pl. 27, pl. 28, fig. 7 (Priesen–Bréšťany, BP).

1866 Ficus tiliaefolia (A. Braun) Heer; Ettingshausen, p. 80, pl. 25, figs 4, 5, 7, 10 (lectotype) (Preschen= Bréšťany, Priesen–Bréšťany, Sobrusan–Zabrušany, BP, BA).

1874 Sterculia dombyopsis (Unger) Schimper, p. 102.

1881 Ficus tiliaefolia (A. Braun) Heer; Velenovský, p. 28, pl. 6, figs 1–4 (Vřesovice–Vřesovice at Louny, NM).

1891 Ficus tiliaefolia (A. Braun) Heer; Engelhardt, p. 162, pl. 9, fig. 25, pl. 10, fig. 9 (SchellenkenŽelénky, missing).

1965 Dombyopsis lobata Unger; Knobloch – Kvaček, p. 134, text-fig. 10 (Želénky, missing).

1971 Dombyopsis lobata Unger; Bůžek, p. 70 (Čermínky, Dolany, UYG).

1999 Dombyopsis lobata Unger; Hurník – Kvaček, p. 653, pl. 4, figs 2–3 (Skyřice, MM).

2000 Dombyopsis lobata Unger; Kvaček – Hurník, p. 13, pl. 5, fig. 12, text-figs 1.17, 3.7 (Vřesovice at Louny, Želénky, Jirášek Mine, Dobřice, Svinčice, Dolany, DB, NM, MM, partly missing).

2000 Dombyopsis lobata Unger; Sakala, p. 62, pl. 6, fig. 5 (Bilina Mine, DB).

2001 Dombyopsis lobata Unger; Hably – Erdei – Kvaček, p. 77–78, pl. 67, fig. 1, pl. 90, fig. 2 (Bilina area, BP – lectotype).

2004a Dombyopsis lobata Unger; Kvaček et al., p. 120, fig. d (Bilina Mine, DB).

Lectotype selected here: BP 59.686.1, Unger, 1850a, p. 447, figured as Ficus dombyopsis 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 (Bréšťany Clay, Bilina 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, unablosed (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, shallow to deeply cordate, apex and lobes wide triangular, blunt, rarely acuminate or apiculate, texture thin. Vena
tion 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 persistent 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 Craiga fruits occur. The type locality of both Craiga bronnii and Dombyopsis lobata is Bilina, namely the clay-pits for ceramic clay (called Bréšťany Clay) formerly situated between Bilina and villages Bréšťany, Bréšťánky and Jenišív 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 Bilina 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 par
ticularly 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, Březánky, scale bar = 10 mm, 2 – type of *Dombeyopsis sidaefolia* Unger (Unger, 1860, pl. 6, fig. 2, as *Ficus tiliæfolia* (A. Braun) Heer), BP 64.300.1, Březánky, scale bar = 10 mm, 3 – extremely small leaf, UUG Če 155a-1015, Čermnìky, scale bar = 10 mm, 4 – larger leaf, UUG Če 155a-1014, Čermnìky, scale bar = 20 mm.
which were assigned originally to *Dombeyopsis sidae-\*f\*olia* Unger and *Ficus tiliae\*f\*olia 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 tiliae\*f\*olia* (A. Braun) Knobloch – Kvaček, formerly known as *Ficus tiliae\*f\*olia* (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” *Banisteria*\*c\*arpum 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 dombeyos\*p\*ysis* Unger, nom. illeg. suprfl. (Unger, 1860). This idea was later followed by Eittingshausen (1866), who misinterpreted *Dombey-\*p\*ysis lobata* for *Ficus tiliae\*f\*olia* (A. Braun) Heer (= *Byttneriophyllum tiliae\*f\*olia* (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) *Dombey-\*p\*ysis lobata* with *Sierculia, 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 *Craiga*). However, the generic distinction is difficult on the basis of epidermal anatomy due to uniform structural traits and their variation within one genus. *Craiga 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 hairy (Kvaček – Worobiec – Worobiec in prep.). Only by a regular association of *Dombeyopsis lobata* with *Craiga* fruits we can assume that this is the foliage of the same plant. The extant species of *Craiga* differ in mostly truncate (*Craiga yunnanensis*) to narrow cuneate leaf basis (*Craiga kwangsiensis*) and always non-lobed ovate lamina. There is a variation in leaf margin from distinctly to indistinctly simple dentate (most populations of *C. yunnanensis* 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:** Bilina–Duchcov area, Břešťany, Břežánky, Jenišův Újezd, former Jirášek Mine, former Maxim Gorkij Mine, now Bilina Mine, Želěnky–Zabrušany, Svinčice, Dobrčice; Louny area, Všovice, Nečichy; Most area, Skyrice; Žatec–Chomutov area, Čermínlky, Dolany.

**Craiga bronni** & *Dombeyopsis lobata* whole plant concept

Fig. 6

Like the taxonomic position of the *Craiga* 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 *Craiga* in the Late Miocene volano-clastics 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 *Dombey-\*p\*ysis lobata* is the best candidate, at least for the European populations, to be combined into the whole plant of *Craiga bronni* as a morpho-taxon of leaves (Kvaček, 1993). Now the European sites of *Craiga* fruits numbering over 70 (Kvaček – Akhmetiev – Manchester in prep.) yielded in 80% cases also leaves of *Dombeyopsis 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 parautocbonous assemblages, where no other tilioid leaves co-occurs. 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 *Craiga* could easily reach depositional sites far from the tree. It is particularly the case of allochthonous delta deposits in the Bilina area (higher fossiliferous horizons in the Bilina Mine), where fruit valves are common, but they
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 *Plaskerisa* 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 bronni* 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 *Intratripropollenites*-type. Zetter (in Kvaček et al., 2002) showed a great similarity between the fossil pollen obtained from flower buds of *Craigia bronni* 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,
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 tiloid 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 auteurology**

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 Libkovic Member. The floras of both areas contain *Craigia*. They are very similar to each other, the former having more frequent ferns (*Woodwardia*, *Pro nephrium* – Bůžek, 1971), the latter including more therophile elements, particularly sabaloid and calamoid palms (Kvaček et al., 2004b). The index fossil *Schenk iella 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 Crai gia bronni & Dombeyopsis lobata plant with Taxodium, Quasisequoia, Glypto tobus 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 wet- land forest vegetation in back swamp along streams and in deltas on clayey and silt flat 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 trees (Quercus rhenana, Myrica liguinitum, Lauraceae, Trigono balanopsis) as well as frequent pine fossils is typical of the Břešťany Clay, the type horizon of Craigia bronni 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 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 para- tropical 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 Arct- ic deciduous forests. As comparative studies of the near- est living relatives progress, similar cases of such Ter-tiary relics have been found, which possibly changed autecology during the Cenozoic (Kvaček submitted).

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

Mostecká páně je místem nejvíce koncentrace fosilních nálezů reliktového rodu *Craiga*, dnes přezívajícího jen na několika místech v jižní Číně a severním Vietnamu. Také odtud bylo poprvé popsan druh *Craiga bronnii* (jako *Ulmus bronnii*) založený na plodních zbytkových podobných jilmovým známkům. Tato konvergence i s řadou jiných křídlatých plodů vedla v minulosti k mnoha mylných systematickým interpretacím. Po objevení celých plodů – pětičtřicenných tobolků a souběžných nálezů květních poupát není dnes pochybný o jejich příslušnosti k zmíněnému reliktovému rodu z čeledi Malvaceae, podčeledi Tiliaeidae. Často související výskyt listů, řazených k morfologické jednotce Dombeysia lobata, dovoluje dnes charakterizovat celou tuto fosilní rostlinu včetně detailů květů, objevených v mostecké pánvi a pylu. Spodnomiocenní evropský zástupce rodu *Craiga*, alespoň podle nahrádění jeho fosilních zbytků v uhelné facii, byl strom snášející bázně prostředí spíše obdoubných porostů vrbice a vrbicích, mohou se výrazně ošklivit od dnešního příbuzného zvířecího zástupce, *Craiga yunnanensis*, přezívajícího v horách jižní Číny a severního Vietnamu v sušších podmínkách parapatrického až subtroppického klimatu v letech složených převážně ze vzdývečených zástupců bukovité.