Foliage and seeds of malvalean plants from the Eocene of Europe

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New malvalean plants, based on foliage and seeds, are reported from the Eocene of Germany (Messel), the Czech Republic (Kučlín) and Hungary (Lábatlan). A new morphogenus *Byttneriopsis* Kvaček & Wilde morphogen. nov. is provided for Eocene foliage with affinities to the Malvales Juss. fam. Malvaceae Juss. *s.l.* The representatives from Messel, based on leaf gross morphology and epidermal anatomy, include *Byttneriopsis daphnogenes* (Ettingshausen) Kvaček & Wilde comb. nov., *Byttneriopsis steuerii* (Engelhardt) Kvaček & Wilde comb. nov. and *Byttneriopsis spiegelii* (Engelhardt) Kvaček & Wilde comb. nov. *B. daphnogenes* also occurs abundantly in Kučlín and *Byttneriopsis steuerii* in Lábatlan. Winged seeds similar to various Malvales, in particular to *Pterospermum* Schreb., co-occur at all three localities and are assigned to *Saportaspermum* Meyer & Manchester as a new morphospecies *Saportaspermum kovacsiae* Kvaček & Wilde sp. nov. • Key words: Malvaceae *s.l.,* Eocene, leaves, epidermal anatomy, seeds, Europe.

KVAČEK, Z. & WILDE, V. 2010. Foliage and seeds of malvalean plants from the Eocene of Europe. *Bulletin of Geosciences 85(1),* 163–182 (9 figures). Czech Geological Survey, Prague. ISSN 1214-1119. Manuscript received October 9, 2009; accepted in revised form November 23, 2009; published online January 21, 2010; issued March 22, 2010.

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Systematics of the Malvales Juss. have recently undergone significant modifications. Following exclusion of the Elaeocarpaceae Juss. ex DC., most of the members of this order have been clustered into a single family, Malvaceae Juss. *s.l.* (Bayer *et al.* 1999, Bayer & Kubitzki 2003, Soltis *et al.* 2005) or split into a larger number of families, namely Sterculiaceae (DC.) Bartl., Pentapetaceae Berch. & J. Presl, Byttneriaceae R. Br., Durionaceae Cheek, Tiliaceae Juss., Brownlowiaceae Cheek, Sparmanniaceae J.G. Agard., Helicteraceae J.G. Agard., Malvaceae Juss. *s.s.* and Bombacaceae Kunth. (Cheek 2006, Heywood *et al.* 2007). As documented by its pollen (for review see Krutzsch 2004), the malvalean group has a considerable geological history. Less straight-forward evidence has been offered by megafossils, in particular foliage. Recently published studies have mostly concentrated on fruits and associated leaves of the Tilioideae Arn. (Manchester 1994, Bůžek & Kvaček 1994, Kvaček & Walther 2004 – *Tilia* L.; Kvaček *et al.* 2005 – *Craigia* W.W. Smith & Evans), while only a few of the remaining megafossils of the malvalean type have been critically re-evaluated (Kvaček 2006, Worobiec *et al.* work in progress). In the present study we have focused on the leaf and seed compression and impression material from three European sites of Middle and Late Eocene age (Fig. 1) – Messel in Germany (for review see Wilde 1989, 2004, 2005), Lábatlan in Hungary (Kovács 1959, 1961; Erdei & Rákosy 2009) and Kučlín in the Czech Republic (for review see Kvaček 2002). The material from Messel offers an opportunity to reveal cuticular structures, which may be helpful in the clarification of systematic affinities. At the same time, gross-morphological variation of the respective leaf morphotypes have also been studied. Furthermore, we have tried to evaluate co-occurring seeds potentially corresponding to the studied foliage.

Material and methods

The oil shale deposited in the maar lake of Messel at Darmstadt in Hesse, Germany, belongs to a world-famous "Lagerstätte", now recognized as a World Heritage Site of fossil biotas (Wilde 2004, 2005; Collinson *et al.* 2010). The abandoned oil shale mining pit, now under State Protection, has yielded numerous animal and plant fossils. The excellent preservation of leaf compressions, due to the bituminous content, allows detailed studies of anatomy and gross morphology. The rarer three-dimensional fruit and seed fossils, also have preserved anatomical details and flowers which are suitable for analyses of pollen *in situ* (Schaarschmidt & Wilde 1986, Wilde & Schaarschmidt 1993).

The fossil-bearing sediment is fine-grained shale containing high concentrations of microscopic algae (Goth

DOI 10.3140/bull.geosci.1170

Figure 1. Geographical position of the localities.

1990). The age of the site has been determined, mainly based on palynology, as early Middle Eocene (Lenz *et al.* 2007). Plant fossils have been known from there since Chelius's (1886) first report. The flora was then described by Engelhardt and posthumously edited by Menzel (Engelhardt 1922). Only after the Second World War a team of scientists from the Senckenberg Museum, Frankfurt/M. began intensive field collections and devised new techniques of preparation with ultrasonic tools, investigation and conservation of plant fossils in glycerol. At the same time, fluorescence microscopy was introduced as a most successful observation technique for these plant fossils (Schaarschmidt 1982). Sturm (1971) and Wilde (1989) began investigations of leaf epidermal anatomy using maceration techniques. Collinson (1988) undertook preliminary surveys of fossil fruits and seeds. The investigations of the fossil flora of Messel have attracted several palaeobotanists to study plant macrofossils from the same location (*e.g.*, Manchester *et al.* 1994, 2007; Wilde & Manchester 2003; Wilde & Frankenhäuser 1999; Wilde *et al.* 2005; Smith *et al.* 2009, in press) and these studies are still continuing at the present time.

The collections from Messel are housed partly in the Museum of Darmstadt (MDAR), where most of the original and type specimens published by Engelhardt (1922) are also preserved, and in the Senckenberg Museum, Frankfurt/M. (SM.B). Plant and animal fossil material is also scattered among other institutions, *e.g.*, in the museum at the Messel site and partly in private collections. The type material described by Engelhardt (1922) is kept in MDAR as dry slabs, while most of the specimens at the Senckenberg Museum are submerged in glycerol. Both kinds of the fossil foliage yielded cuticles when macerated with Schulze's solution, the latter were also observed using fluorescence microscopy (Wilde 1989).

The locality of Kučlín in North Bohemia was discovered in the 19th century on the Trupelník Hill (Trippelberg) in the vicinity of Bílina. Radiometric dating indicates it to be Late Eocene (see Kvaček 2002). The fossiliferous rock, a hard beige-colored diatomite, crops out at present in several places at the top of the hill. In addition to the main site, whitish shale containing the same flora crops out beneath the diatomite in the Dead Hill (Mrtvý vrch, Totenberg) at Kučlín. The fossils treated by Ettingshausen (1866–69) were mostly excavated on the slope of the Trupelník Hill from a portion of the diatomite layer shifted by landslide from the original position. The diatomite is deeply weathered and oxidized, so that the fossils are whitish, yellowish impressions without carbonized substance and cuticle remains. Venation is mostly lightly impressed in the rock with many fine details; its reproduction is, however, possible only under very oblique light. Most fossils from Kučlín were concentrated in the so-called Lobkowitz's collection in the castle in Bílina and later sold to Budapest (Hably *et al.* 2003) including the type and original material published by Ettingshausen (1866–1869). This and later collections made at that time are now housed in the Hungarian Natural History Museum, Budapest (numbers prefixed by BP) and the Austrian Geological Survey (Geologische Bundesanstalt) in Vienna (GBA). Other material excavated at Kučlín during the 19th and 20th centuries is distributed in various collections, namely the National Museum, Prague (specimen numbers prefixed by NM-G), Czech Geological Survey (CGS), Naturhistorische Sammlungen Senckenberg, Dresden – Museum für Mineralogie und Geologie Dresden (MMG) and the Headquarters of the Bílina Mines (DB).

Lábatlan is a site of Middle Eocene flora in Hungary (Kovács 1959, Hably 1985). The fossiliferous clay that once cropped out in an abandoned clay pit, represents a clay lens within a substantial freshwater sandy-gravel layer above the Early Eocene limestone (Kovács 1961; Erdei & Rákosi 2009). The collected impressions and compressions of plant remains are in many cases fragmentary. Although the leaves are covered by carbonized matter, the specimens studied have yielded only poor cuticle fragments on maceration (Kvaček *in* Knobloch *et al.* 1996). The whole collection is housed at present in the Hungarian Geological Survey (MAFI) in Budapest.

We have studied living material of the Malvales for comparison, mainly in herbaria of the Museum National d'Histoire Naturelle, Paris (P), British Museum of Natural History, London (BM), Royal Botanic Gardens, Kew (K) as well as in many other places and botanical gardens. The reference collection of epidermal preparations used in this study is housed in the Faculty of Science, Charles University (PRC).

Systematic descriptions

Order Malvales Juss. *ex* Bercht. & J. Presl

The previous concept of the Malvales, including several families with partly equivocal circumscription (Takhtajan

1980, 1997; Cronquist 1988; Thorne 1992), has been revised on account of a complex cladistic analysis (Judd & Manchester 1997) and molecular studies (Alverson *et al.* 1998, 1999; Worberg *et al.* 2009). By excluding Elaeocarpaceae Juss. *ex* DC. from the Malvales, the system of the Malvaceae Juss. *sensu lato* has become more natural and the reorganization of subordinate families into subfamilies (Bayer & Kubitzki 2003) more useful. However, one of the latest versions of the malvalean plant systematics (Heywood *et al.* 2007) again favours the restricted concept of ten families, more restricted than previously. We adhere to Malvaceae *s.l.*, which is in current use (Bayer & Kubitzki 2003, von Balthazar *et al.* 2006; Worobiec *et al.* work in progress) and seems to be more useful in palaeobotanical practice. It is then not surprising that the family Malvaceae *sensu lato* is recognizable in the fossil state, even as fossil wood (see Manchester *et al.* 2006), although it is far from uniform with respect to leaf morphology (and also fruits, seeds and pollen, *etc*.). The typical actinodromous venation is well represented in the majority of the groups, but venation alone is not sufficient to prove malvalean affinities because such a venation type is found abundantly elsewhere among dicots. This was also the reason for much confusion in previous palaeobotanical research which was based on gross-morphology alone. Several palmately-veined leaf morphotypes which turned to be malvalean were thus assigned to diverse families, such as Moraceae Link. (*Ficus* L., *Cecropia* Loefl. – *e.g.* Heer 1856, 1859; Ettingshausen 1866), Scrophulariaceae Juss. (*Paulownia* Siebold & Zucc. – *e.g.* Laurent 1904–1905), Cornaceae Dum. (*Alangium* Lam. – Kryshtofovich & Borsuk 1939), *etc.* More promising criteria are provided by using a combination of fine venation (Tanai 1989) and epidermal characters, in particular the indumentum (*e.g.*, Knobloch & Kvaček 1965, Worobiec 2003, Worobiec *et al.* work in progress). Preliminary comparative studies on epidermal anatomy of various representatives of the Malvaceae *s.l.* (Worobiec 2003, Worobiec *et al.* work in progress, Kvaček own observations) suggest that barrel-shaped or clavate glandular trichomes are typical of many malvalean genera and thus are of diagnostic value. On the other hand, other epidermal criteria, such as stomatal type, non-glandular trichomes, the shape of epidermal cells, etc., usually do not circumscribe the natural generic units as understood in extant Malvales. Therefore, the leaf fossils should be assigned to more general categories – morphogenera, even if details of venation and cuticular structures are available.

Considering priority, the earliest published name for such leaves is *Dombeyopsis* Unger (1850a). The extent of this morphogenus has varied greatly through time (Unger 1850a, Massalongo 1854, Schimper 1874), originally also including dubious and clearly non-malvaceous leaf types such as *Cercidiphyllum* Siebold & Zucc. Therefore Krassilov (1979) strongly rejected *Dombeyopsis* since its name was not typified by an illustration when published (Unger 1850a). We suggest restricting this morphogenus to include only the type-bearing species *Dombeyopsis lobata* Unger (type from the Early Miocene Břešťany Clay in the Bílina area in North Bohemia – Kvaček 2004) whose epidermal characters correspond to the Malvaceae *s.l.* Other occurrences of *Dombeyopsis lobata* (incl. *Dombeyopsis dechenii* C. Weber and many other synonyms) are found widespread in the Oligocene, Miocene and even Pliocene of Europe (Worobiec *et al.* work in progress). The malvalean affinity of these records is confirmed by epidermal anatomy (*e.g.*, Mai & Walther 1991, Walther & Kvaček 2007, Kvaček *et al.* 2008) and/or co-occurrence of fruits of *Craigia bronnii* (Unger) Kvaček, Bůžek & Manchester (Kvaček 2004, Kvaček *et al.* 2005). The other existing malvalean morphogenera for leaves, such as *Byttneriophyllum* Givulescu *ex* Knobloch & Kvaček (1965) and *Plafkeria* Wolfe (1977) (incl. *Actinovena* Tanai, 1989) differ in having asymmetric primary venation of the leaf blade. The current concepts for the listed genera are also narrow and restricted to a few species. *Byttneriophyllum* includes only the species *B. tiliifolium* (A. Braun) Knobloch & Kvaček, which regularly co-occurs with fruits of the "giant maple" *Banisteriaecarpum* Kräusel. *Plafkeria*, on the other hand, often co-occurs in North America and East Asia with fruits of *Craigia oregonensis* (Arnold) Kvaček, Bůžek & Manchester (Kvaček *et al.* 2005). Relying on the symmetry of the basal venation (but not on the symmetry of the leaf blade) and epidermal characters supporting malvalean affinities, we now define a new morphogenus separated from *Dombeyopsis*, *Byttneriophyllum* and *Plafkeria* in gross morphology, for non-lobate entire-margined leaves occurring in the European Eocene.

Family Malvaceae Juss. *nom. cons. s.l.*

Morphogenus *Byttneriopsis* Kvaček & Wilde morphogen. nov.

Description. – Leaves simple, with usually a long, partly geniculate petiole; lamina non-lobate, entire-margined; venation triveined to palmate with all primaries arising directly from the base of the lamina, number of lateral primaries ± equal on either side of the midrib, tertiary and higher-order veins between primaries percurrent or forked, forming a regular net pattern, areoles reticulate, without free ending veinlets; indumentum including barrel-shaped glandular trichomes or their bases and rarely, thickly cutinized rosette-like complex bases of stellate trichomes.

Type designated here. – *Byttneriopsis spiegelii* (Engelhardt) Kvaček & Wilde comb. nov. (*Catalpa spiegelii* Engelhardt).

Remarks. – The detailed circumscription of this morphogenus is mainly based on the rich, well preserved material from the Middle Eocene of Messel which enables studies of epidermal characters to be undertaken. Three malvalean leaf morphotypes connected with transitions can be distinguished in this plant taphocoenosis. The critical character supporting malvalean affinities are specific types of trichomes and their bases. Most typical are simple rounded to elliptic bases, on which remains of barrel-shaped polycellular glandular trichomes are occasionally preserved. They correspond to a general form of such trichomes commonly distributed throughout the Malvales. Another kind of pubescence is represented by complex trichome bases as sometimes seen in the material from Messel, which may have carried stellate-multiradiate trichomes. The latter are also characteristic of many members of the malvalean alliance (*e.g. Eriolaena* DC).

The newly established morphogenus *Byttneriopsis* may be similar in overall gross morphology to the two other currently used malvalean foliage morphogenera *Byttneriophyllum* and *Plafkeria*, which differ especially in the asymmetry of the basal venation. The distinction between *Byttneriopsis* and *Dombeyopsis* used by earlier authors in a different sense is less clear. The latter is accepted here in a restricted sense as suggested by Kvaček (2004), viz. to include only the species *D. lobata* typically with trilobate leaves with occasionally undulate to dentate margins and a different abaxial epidermis with a dense indumentum of stellate trichomes. Other leaf forms similar to *Byttneriopsis* are those of "*Ficus*" *truncata* Heer *sensu* Bůžek (1971), which are also of malvalean affinity and have recently been discussed as possibly related to *Reevesia* Lindl. (Kvaček 2006). They differ in having a much less regular tertiary and higher-order venation between the primaries and secondaries (Worobiec 2003; Worobiec *et al.* work in progress).

The delimitation of the morphospecies within *Byttneriopsis* as described below is complicated by considerable variability in gross morphology and epidermal structures in the Messel specimens, probably due to a differentiation into mesomorphic shade and more xeromorphic sun leaves. The same variation in gross morphology has been found in the population from Kučlín, from which evidence of epidermal anatomy is not available. In addition to gross morphology, we have also considered other diagnostic characters, *e.g.* stomata (type, form and size), epicuticular sculpture (absence or kind of the striation if present), and the distribution and frequency of trichomes/trichome bases, and distinguished three morphospecies, *Byttneriopsis daphnogenes* (Ettingshausen) Kvaček & Wilde comb. nov., *Byttneriopsis steuerii* (Engelhardt) Kvaček & Wilde comb. nov., and *Byttneriopsis spiegelii* (Engelhardt) Kvaček & Wilde comb. nov. They are probably formal as they are connected at Messel with transitions and may in fact derive from one plant with variable foliage. *B. daphnogenes* also occurs abundantly at Kučlín, while *Byttneriopsis steuerii* is common at Lábatlan and *Byttneriopsis spiegelii* is endemic to Messel.

Byttneriopsis daphnogenes (Ettingshausen) Kvaček & Wilde comb. nov.

Figures 2A–J, 3A–E, 7A–H, 8A, B

1866 *Ficus daphnogenes* Ettingshausen, p. 77 (basionym), pl. 22, figs 1, 2 (lectotype), 8, 9 (Kučlín).
1866 *Ficus goeppertii* Ettingshausen, p. 73, partim, pl. 19, figs 1, 2 (Kučlín).
1866 *Ficus reussii* Ettingshausen, p. 79, pl. 22, figs 3, 4, 7, 10 (Kučlín, Kostomlaty).
1866 *Ficus rueminianum* Heer *sensu* Ettingshausen (non Heer), p. 76, pl. 22, fig. 5 (Kučlín).
?1922 *Piper europaeum* Engelhardt, p. 33, pl. 5, fig. 4 (Messel).
?1922 *Ficus undulata* Engelhardt, p. 41, pl. 8, fig. 1 (Messel).
1922 *Ficus angustifolia* Engelhardt, p. 41, pl. 8, fig. 8 (Messel).
1922 *Ficus eocaenica* Engelhardt, p. 42, pl. 8, fig. 5 (Messel).
1922 *Ficus ovatolanceolata* Engelhardt, p. 47, pl. 9, fig. 2 (Messel).
1922 *Ficus wetteravica* Ettingshausen *sensu* Engelhardt (non Ettingshausen), p. 46, pl. 10, fig. 4 (Messel).
1922 *Ficus thaliae* Unger *sensu* Engelhardt (non Unger), p. 45, pl. 10, fig.7 (Messel).
1922 *Ficus michelotii* Watelet *sensu* Engelhardt (non Watelet), p. 45, pl. 10, fig. 8 (Messel).
1922 *Ficus ovatifolia* Engelhardt, p. 46, pl. 10, fig. 9 (Messel).
1922 *Ficus messelensis* Engelhardt, p. 47, pl. 11, figs 3, 4 (Messel).
1922 *Ficus titanum* Ettinsghausen *sensu* Engelhardt (non Ettinsghausen), p. 48, pl. 12, fig. 3 (Messel).

Figure 2. *Byttneriopsis daphnogenes* (Ettingshausen) Kvaček & Wilde comb. nov., Messel. • A – long petiolate leaf with rounded base and without inflated attachment to the base, *i.e.* pulvinus refigured from Wilde (1989, pl. 6, fig. 4, as ?Illiciaceae sp.), SM.B Me 929, × 1. • B – detail of leaf base from the previous specimen, × 2.5. • C – elongate form with cuneate base and prominent pulvinus, SM.B Me 3463, × 0.8. • D – detail of leaf base from the previous specimen, × 3. • E – elongate leaf with slightly asymmetrical base and incomplete petiole, SM B Me 1452, × 1. • F – elongate leaf with oblique pulvinate petiole, SM.B Me 3297, × 1. • G – twig with broadly ovate long petiolate leaf, SM.B Me 1681, × 0.7. • H – detail of leaf base from the specimen shown in figure G, × 4. • I – narrow, ovate long petiolate leaf with less prominent pulvinus, SM.B Me 851, × 1. • J – rounded deformed leaf, SM.B Me 1705, × 1.5. • K – *Byttneriopsis steuerii* (Engelhardt) Kvaček & Wilde comb. nov., Messel; broad leaf with subcordate base, SM.B Me 748, × 1. (A lower quality of illustrations in Fig. 2 is due to photography through glycerol in which the plant fossils are kept to prevent damage.)


A
B
C
D
E
F
G
H
I
J
K

1922 *Ficus daphnogenoides* Engelhardt, p. 48, pl. 13, fig. 4 (Messel).
1922 *Grewia tenuifolia* Engelhardt, p. 89, pl. 29, fig. 3, pl. 30, fig. 5 (Messel).
1922 *Sterculia grandifolia* Engelhardt, p. 88, pl. 29, fig. 5 (Messel).
?1922 *Phaseolites eocaenica* Engelhardt 1922, p. 111, pl. 37, fig. 9 (Messel).
?1922 *Erythrina phaseolites* Engelhardt 1922, p. 111, pl. 37, fig. 18 (Messel).
1989 *Ficus* sp. *sensu* Wilde, p. 37, pro parte, pl. 6, figs 1–3 (Messel).
1989 ?Illiciaceae sp. *sensu* Wilde, p. 40, pl. 6, figs 4–6 (Messel).

Diagnosis emended. – Leaves simple, entire-margined, non-lobate, often long petiolate, petiole often pulvinate at the lamina base and geniculate, lamina slender elongate to ovate, at the base cuneate to rounded, sometimes slightly asymmetrical, venation brochidodromous, typically triveined; trichomes glandular barrel-shaped or only their simple bases dispersed on the abaxial leaf side together with rare, thickened, rosette-like polycellular trichome bases.

Lectotype designated here. – BP 55.2477.1 (Ettingshausen 1866, pl. 22, fig. 2, illustrated as *Ficus daphnogenes* and re-illustrated in Hably *et al.* 2001 and here Figs 3A, E) – Kučlín, North Bohemia, Late Eocene.

Additional material. – Messel – SM.B Me 388, 745, 746, 779, 824, 840, 851, 870, 905, 908, 911, 917, 928, 929, 965, 973, 975, 1355, 1388, 1400, 1419, 1424, 1428, 1430, 1432, 1444, 1448, 1452, 1473, 1542, 1548, 1585, 1594, 1595, 1642, 1643, 1651, 1680, 1681, 1705, 1714, 1736, 1755, 1863, 1923, 1925, 1928, 3001, 3185, 3297, 3327, 3336, 3345, 3463, 3466, 3563, 3582, 3913; MDAR Me 222 (*Sterculia grandifolia* Engelhardt, 1922, p. 88, pl. 29, fig. 5 HOLO), ?Me 1906 (*Phaseolites eocaenica* Engelhardt, 1922, p. 111, pl. 37, fig. 9 HOLO), Me 1998 (*Ficus ovatolanceolata* Engelhardt, 1922, p. 47, pl. 9, fig. 2 HOLO), Me 2014 (*Ficus subdimidiata* Engelhardt, 1922, p. 47, pl. 13, fig. 6), Me 3516 (*Ficus messelensis* Engelhardt, 1922, p. 47, pl. 11, fig. 3), Me 3520 (*Ficus eocaenica* Engelhardt 1922, p. 42, pl. 8, fig. 5); Kučlín – BP 55.2329.1 (*Ficus rueminianum* Heer *sensu* Ettingshausen, 1866, p. 76, pl. 22, fig. 5), BP 55.2358.1 (*Ficus reussii* Ettingshausen, 1866, p. 79, pl. 22, fig. 10), BP 55.2481.1 (*Ficus daphogenes* Ettingshausen, 1866, p. 77, pl. 22, fig. 2), DB KUC-53, 160, 199, 200, CGS CB 13 and many other sine numero.

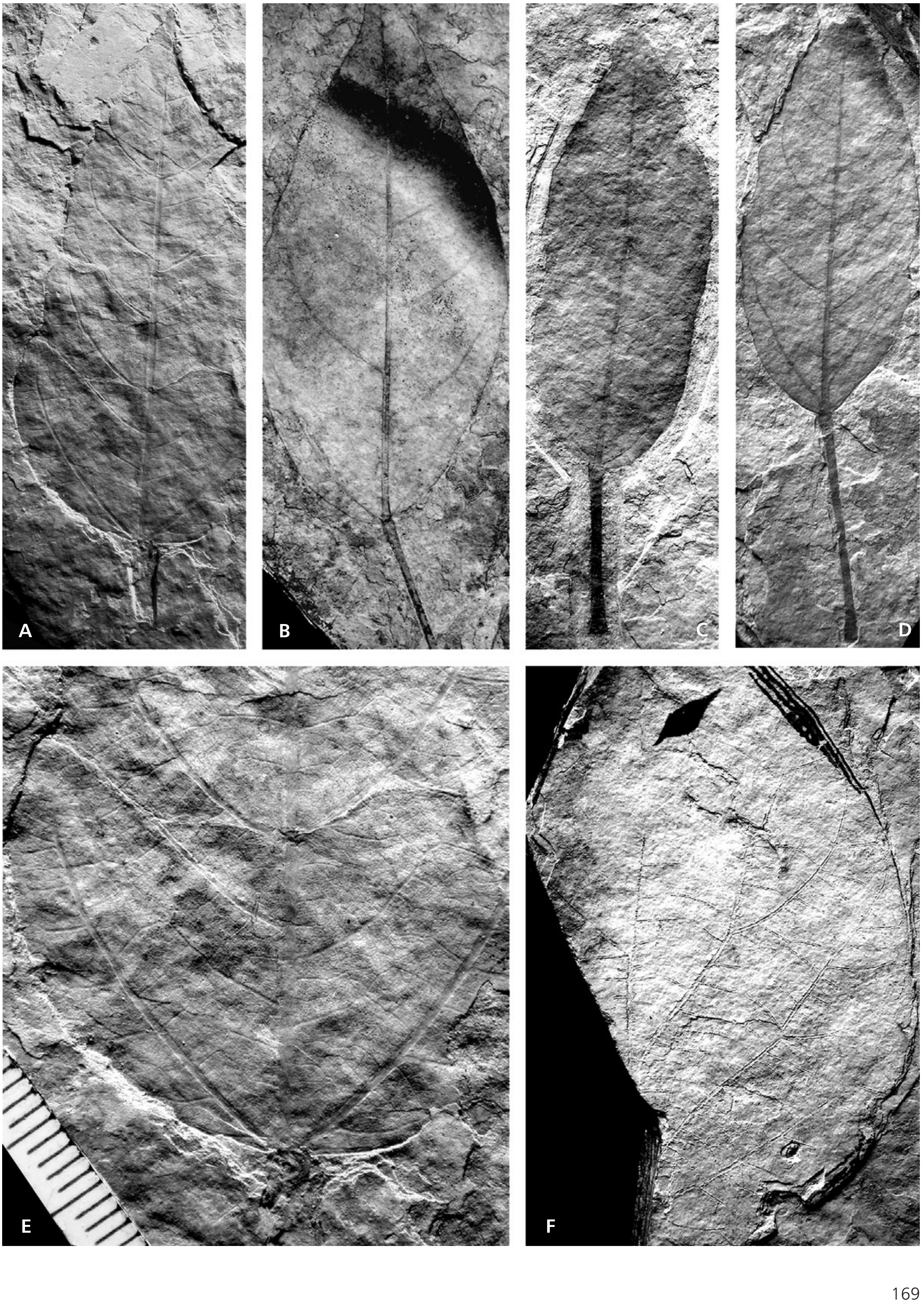
Description. – Leaves alternate, simple, long petiolate, variable in lamina shape and size as well as in epidermal structure, petiole up to 4 cm long, often pulvinate at the attachment to the lamina and geniculate; lamina entire-margined, hypostomatic, elongate to narrow ovate (length/width ratio usually greater than 1.5), 4 to 6 cm or more in length, 2.5 to 4 cm wide, symmetrical to moderately asymmetrical, cuneate to rounded at the base, blunt acute at the apex, texture chartaceous to coriaceous, venation brochidodromous, basally triveined, midrib straight or slightly bent, lateral primaries thin, slightly bent, rarely reaching more than half, but usually one third of the lamina length or less , secondaries irregularly alternate, arising at uneven distances of about 1–3 cm, at an angle of 30–45°, bent, tertiaries percurrent or forked, almost perpendicular to the secondaries, areoles mostly quadrangular without veinlets; cuticles medium thick, adaxial cuticle often slightly granular-striated, reflecting polygonal (4–6-sided) cells, 13–28 μm in diameter, anticlinal walls straight or almost straight, abaxial cuticle thinner, smooth except for slight circumstomatal striation, non-modified cells similar to those of the adaxial cuticle, stomata in intercostal areas only, dense, circular to widely oval, partly with polar I-pieces, ledges double thickened, surrounding widely open aperture, stomatal type not always recognizable, incompletely to regularly cyclocytic, rarely anomocytic, trichome bases of two types: simple rounded, 10–15 μm in diameter, surrounded by radial subsidiary cells, partly with remains of obconical basal cell, exceptionally with the barrel-shaped distal part up to 25 μm wide composed of two layers of small segment cells, longitudinally orientated, scattered to densely dispersed all over the abaxial epidermis; complex rosette-like thickly cutinized bases of stellate trichomes up to 40 μm in diameter, solitary on veins.

Byttneriopsis steuerii (Engelhardt) Kvaček & Wilde comb. nov.

Figures 2K, 3F, 4A–D, 5E, 6C–E, 8C, D

1922 *Pterospermum steuerii* Engelhardt, p. 89 (basionym), pl. 27, fig. 3 (Messel).

Figure 3. *Byttneriopsis daphnogenes* (Ettingshausen) Kvaček & Wilde comb. nov., Kučlín. • A – lectotype re-illustrated from Ettingshausen (1866, pl. 22, fig. 2, as *Ficus daphogenes*), standard form with rounded base and incomplete pulvinate petiole, BP 55.2477.1, × 1.5. • B – elongate form with less distinctly pulvinate petiole. ČGS ČB 13, × 1. • C – elongate form with stout petiole, DB KUC 52, × 1. • D – extremely long petiolate elongate leaf, DB KUC 53, × 1. • E – detail of leaf base from the lectotype shown in Fig. 3A, × 3. • F – *Byttneriopsis steuerii* (Engelhardt) Kvaček & Wilde comb. nov., Kučlín; fragment of a broad subcordate leaf, × 1.


A
B
C
D
E
F

1922 *Macropiper rotundifolium* Engelhardt, p. 33, pl. 6, fig. 2 (Messel).
1922 *Ficus populifolia* Engelhardt, p. 44, pl. 10, fig. 5 (Messel).
1922 *Ficus planicostata* Lesquereux *sensu* Engelhardt (non Lesquereux), p. 45, pl. 10, fig. 6 (Messel).
1922 *Ficus tiliifolia* A. Braun *sensu* Engelhardt (non A. Braun), p. 49, pro parte, pl. 11, fig. 5 (Messel).
1922 *Ficus rotundifolia* Engelhardt, p. 49, pl. 11, fig. 6 (Messel).
?1922 *Ficus subdividiata* Engelhardt, p. 47, pl. 13, fig. 6 (Messel).
1922 *Populus mutabilis* Heer *sensu* Engelhardt (non Heer), p. 61, pl. 18, fig. 6 (Messel).
1922 *Grewia microcoides* Engelhardt, p. 89, pl. 30, fig. 9 (Messel).
1922 *Grewiopsis* sp. sensu Engelhardt, p. 90, pl. 30, fig. 10 (Messel).
?1959 *Grewiopsis inaequalis* É. Kovács, p. 136, fig. 3 (Lábatlan).
1959 *Byttneria apiculata* É. Kovács, p. 137, figs 4–6 ("*Buettneria*") (Lábatlan).
1961 *Byttneria apiculata* É. Kovács *sensu* É. Kovács, p. 474, pl. 1, figs 4, 5 (Lábatlan).
1989 *Byttneriophyllum tiliifolium* (Al. Braun) Knobloch & Kvaček *sensu* Wilde [non (Al. Braun) Knobloch & Kvaček], p. 71, pl. 20, figs 4a–c (Messel).

Diagnosis emended. – Leaves similar to *Byttneriopsis daphnogenes* both in detailed venation and epidermal anatomy, but lamina broadly ovate to suborbicular, at the base truncate to cordate, venation triveined tending towards actinodromy, with 2–4 additional lateral primaries.

Holotype designated here. – MDAR Me 1637 (*Pterospermum steuerii* Engelhardt, 1922, p. 89, pl. 27, fig. 3 and re-illustrated here in Fig. 4C, D and cuticle in Fig. 8D) – Middle Eocene, Messel.

Additional material. – Messel – SM.B Me 749, 908, 1428 (*Byttneriophyllum tiliifolium* (Al. Braun) Knobloch & Kvaček *sensu* Wilde, 1989, p. 71, pl. 20, fig. 4a–c), 1707, 1893, MDAR Me 3524 (*Grewia microcoides* Engelhardt, 1922, p. 89, pl. 30, fig. 9); Kučlín – DB KUC 51, 218; Lábatlan – MAFI 3448 (L 15), 3476 (L 23), 3486 (L 28) (*Byttneria apiculata* É. Kovács, 1959, p. 137, fig. 4), 3566 (L 150) (*Byttneria apiculata* É. Kovács, 1959, p. 137, fig. 5 counterimpression), 3554 (L 154), 3563, 3588, 3593 (*Byttneria apiculata* É. Kovács, 1959, p. 137, fig. 6), 3695, ?3452 (L 9) and counterimpression 3566 (L 150) (*Grewiopsis inaequalis* É. Kovács, p. 136, fig. 3).

Description. – Leaves simple, long petiolate, petiole often incomplete, partly pulvinate, lamina broadly ovate to suborbicular, up to more than 12 cm long and 10 cm wide, at base truncate, shallowly to deeply cordate, apex bluntly acute to acuminate, venation actinodromous-brochidodromous, typically palmately 5 to 7-veined, ± symmetrical, texture chartaceous; adaxial cuticle smooth, reflecting polygonal cells *ca* 20–25 μm in diameter, with straight to slightly curved anticlines, abaxial cuticle thin, partly faintly striate, composed of non-modified cells *ca* 15–25 μm in diameter with slightly curved anticlines, stomata sub-circular, 15 μm long, with narrow elliptic apertures and less thickened stomatal ledges, stomatal type incompletely cyclocytic to anomocytic, bases of trichomes of the same type as in *Byttneriopsis daphnogenes*, but much rarer or solitary.

Remarks. – *Byttneriopsis daphnogenes* is much more frequent than the more mesomorphic *Byttneriopsis steuerii* in both Messel and Kučlín, while the latter occurs more frequent only at Lábatlan (as *Byttneria apiculata*). The exact separation of the two morphospecies is somewhat vague due to transitions. Although epidermal characters are only known for the material from Messel, we do not hesitate to merge both the Messel, Lábatlan and Kučlín populations into two variable entities on account of similarities in gross morphology. The lectotype of *Byttneriopsis daphnogenes* from Kučlín and other specimens from this Late Eocene locality (Fig. 3A–I) are morphologically indistinguishable from an overwhelming part of the Messel material, comprising mostly triveined forms rounded and symmetrical at the base and long petiolate, often pulvinate at the attachment to the blade; these diagnostic characters may serve as a basis for recognition of these leaf morphotypes elsewhere, *e.g.* in the Eocene site Kostomlaty not far from Kučlín (Ettingshausen 1866, as *Ficus reussii* Ettingshausen). *Byttneriopsis daphnogenes* and *Byttneriopsis steuerii* are similar in the overall variation of lamina shape, compared to the even more variable Miocene *Ficus truncata* Heer (as circumscribed by Bůžek 1971) with cuneate to deeply cordate leaves (see Kvaček 2006). The latter is distinguished by irregular, coarse and wider disposition of tertiary venation and by its epidermal characters (Worobiec 2003; Worobiec *et al.* work in progress).

Byttneriopsis steuerii is morphologically similar to *Pterospermum chattanum* Engelhardt (1922, p. 89, pl. 30, fig. 6), which belongs to the Lauraceae and differs in subbasal secondaries and leaf anatomy (internal oil cells, different simple trichome bases).

Byttneriopsis spiegelii (Engelhardt) Kvaček & Wilde comb. nov.

Figures 6A–C, 8E, F

1922 *Catalpa spiegelii* Engelhardt, p. 70 (basionym), pl. 22, fig. 1 (Messel).

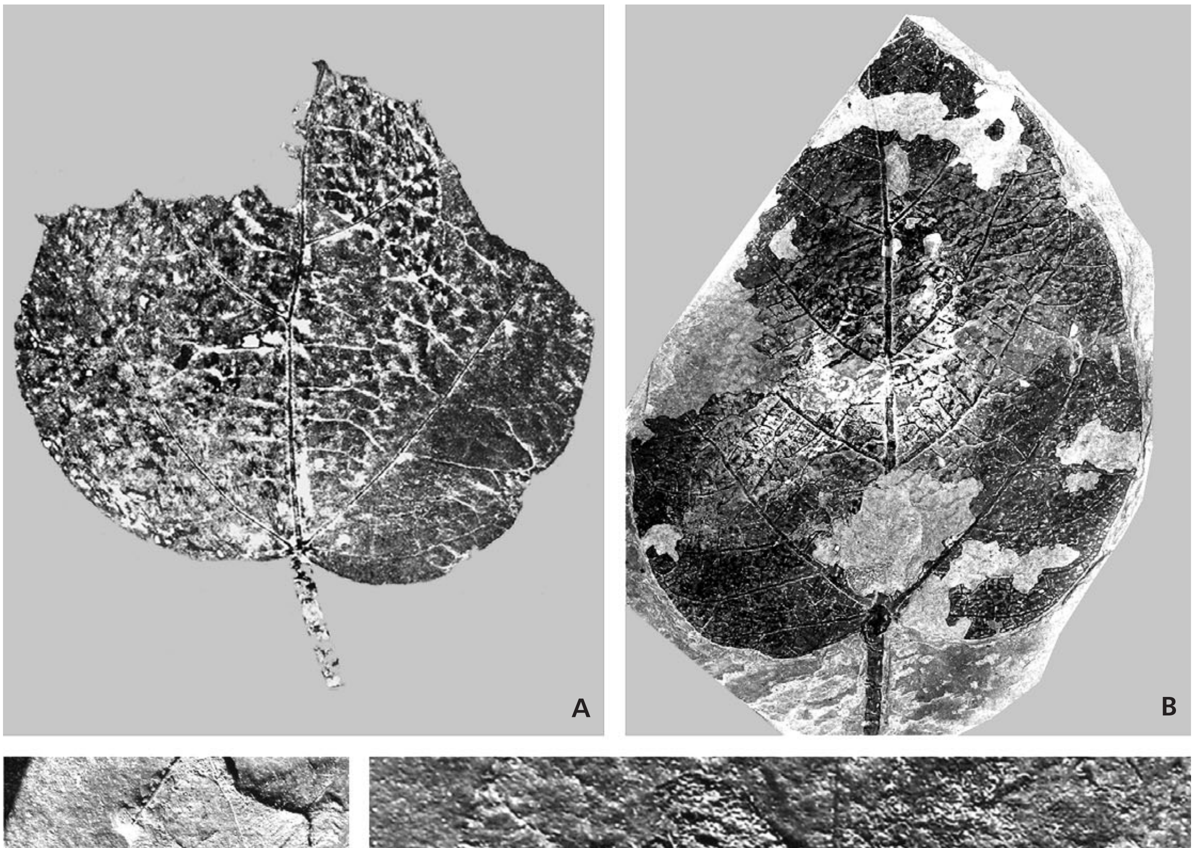


Figure 4. *Byttneriopsis steuerii* (Engelhardt) Kvaček & Wilde comb. nov., Messel. • A – subcordate leaf without pulvinus, SM.B Me 908, × 1. • B – cordate leaf with distinctly pulvinate petiole refigured from Wilde (1989, pl. 20, figs 4a–c, as *Byttneriophyllum tiliaefolium*), SM.B Me 1428, × 0.7. • C – short ovate, petiolate leaf with truncate asymmetrical base and without pulvinus, holotype refigured from Engelhardt (1922, p. 89, pl. 27, fig. 2, as *Pterospermum steuerii*), MDAR Me 1637, × 1.5. • D – detail of the same specimen, × 3.

1922 *Ficus tiliaefolia* (Al. Braun) Heer *sensu* Engelhardt (non (Al. Braun) Heer), p. 49, pro parte, pl. 12, fig. 5 (Messel).
1922 *Cercis grandifolia* Engelhardt, p. 114, pl. 38, fig. 1 (Messel).
?1922 *Cecropia europaea* Ettingshausen *sensu* Engelhardt (non Ettingshausen), p. 60, pl. 18, fig. 3 (Messel).

Holotype designated here. – Specimen No. MDAR Me 3436 (Me027) (Museum Darmstadt) (illustrated in Engelhardt (1922) as *Catalpa spiegelii* Engelhardt, p. 70, pl. 22, fig. 1 and re-illustrated here – Fig. 6A–C and cuticles in Fig. 8E, F) – Middle Eocene, Messel.

Additional material studied. – MDAR Me 79 (*Ficus tiliaefolia* (Al. Braun) Heer *sensu* Engelhardt 1922, p. 49, pl. 12, fig. 5).

Description– Leaves long petiolate, petiole not pulvinate, lamina non-lobate, entire-margined, broadly ovate to orbicular, up to 20 cm wide and over 22 cm long, deeply cordate at base, apex probably convex, venation actinodromous-brochidodromous, typically palmately 5 to 7-veined, ± symmetrical. Adaxial cuticle smooth, reflecting polygonal cells *ca* 20–25 μm in diameter, with straight to slightly curved anticlines, abaxial cuticle faintly striate, composed of non-modified cells *ca* 15–25 μm in diameter with slightly curved anticlines. Stomata subcircular, 15 μm long, with narrow elliptic aperture and unthickened stomatal ledges. Stomatal type anomocytic to incompletely cyclocytic. Solitary rounded trichome bases, rarely distal parts of barrel-shaped glandular trichomes preserved, consisting of a basal funnel-shaped cell and thin-walled multicellular head divided into segments parallel to the trichome length.

Remarks. – *Byttneriopsis spiegelii* co-occurs in Messel with *B. daphnogenes* and *B. steuerii*. We separate these rare, extremely large leaves on account of differences in both gross morphology (deeply cordate forms) and epidermal anatomy (very thin striated abaxial cuticles with indistinctly cutinized stomata). In our opinion, it is very probable that they might represent mere aberrant leaf forms of *B. steuerii*. *Byttneriopsis spiegelii* is similar in gross morphology to the non-lobate entire-margined forms of *Dombeyopsis lobata* (*e.g*., Kvaček 2004, fig. 4.2) in the deeply cordate base of the lamina, a stout stalk, and almost symmetrically disposed primaries, but differs from it in the epidermal anatomy. In contrast to *Byttneriopsis spiegelii*, *Dombeyopsis lobata*, representing foliage of *Craigia bronnii* (Oligocene to Pliocene of Europe, Kvaček *et al.* 2005), has the underside covered by stellate trichomes (Knobloch & Kvaček 1976, Kvaček 2004) while the leaves of *Byttneriopsis spiegelii* are glabrescent. Another common malvalean foliage type known as *Byttneriophyllum tiliifolium* (Miocene to Pliocene of Europe and East Asia), also has a dense cover of stellate trichomes on the abaxial epidermis (Knobloch & Kvaček 1965, Worobiec 2003), but differs decidedly in the typically oblique leaf base and unequally disposed lateral primaries emerging from the midrib.

The associated seeds

Morphogenus *Saportaspermum* Meyer & Manchester

The winged seeds, which were included in this morphogenus (type *S. occidentale* Meyer & Manchester 1997, p. 161, pl. 74, figs 14–20, Oligocene of the John Day Formation, Oregon), are typical of those wings either without or with very feebly visible veins. Contrary to similar seeds of the Pinaceae, the seed body is attached to the wing dorsally, not laterally. In addition to the type described by Meyer & Manchester (1997) from the Oligocene of North America, similar small seeds have been recorded in the Paleogene and Miocene of Europe (see, *e.g.* Bůžek *et al*. 1976, pl. 12, figs 6–9, as "*Embothrium*" cf. *salicinum* Heer from the Oligocene of Markvartice, N Bohemia; Kovar-Eder *et al.* 2004, pl. 15, figs 6–8, as *Saportaspermum* sp. from the Miocene of Parschlug, Styria). Specimens corresponding with the type of the genus (Hably *et al*. 2000) were described under various species names and await taxonomic revision. In one such case, seeds were found in the Lower Miocene of Bílina, North Bohemia in association with the fruits of *Reevesia* (Kvaček 2006). In other cases, affinities are uncertain. Bigger seeds, similar to the new morphospecies described below, occur in the Early Oligocene site of Seifhennersdorf (as *Saportaspermum dieteri* Walther & Kvaček, 2007) and differ only in subtle details (see below). The species differences within *Saportaspermum* are certainly not very pronounced.

Saportaspermum kovacsiae Kvaček & Wilde sp. nov.

Figures 9A–H

1959 *Cedrelospermum* sp. type I *sensu* É. Kovács, p. 140, fig. 7 (Lábatlan, MÁFI).
1959 *Cedrelospermum* sp. type II *sensu* É. Kovács, p. 140, fig. 8 (Lábatlan, MÁFI).
1961 *Cedrelospermum* sp. type I *sensu* É. Kovács, p. 474, pl. 1, fig. 6 (Lábatlan, MÁFI).

Diagnosis. – Seeds winged, with an elliptical to sub-orbicular seed body, strengthened at the base and somewhat pointed at the opposite end, with a single narrow elongate membranaceous wing; surface of the seed body with more or less visible striation from alignment of surface cells. Seed body orientated obliquely to the long axis of the wing (30–40°); one of the lateral margins straight, the other

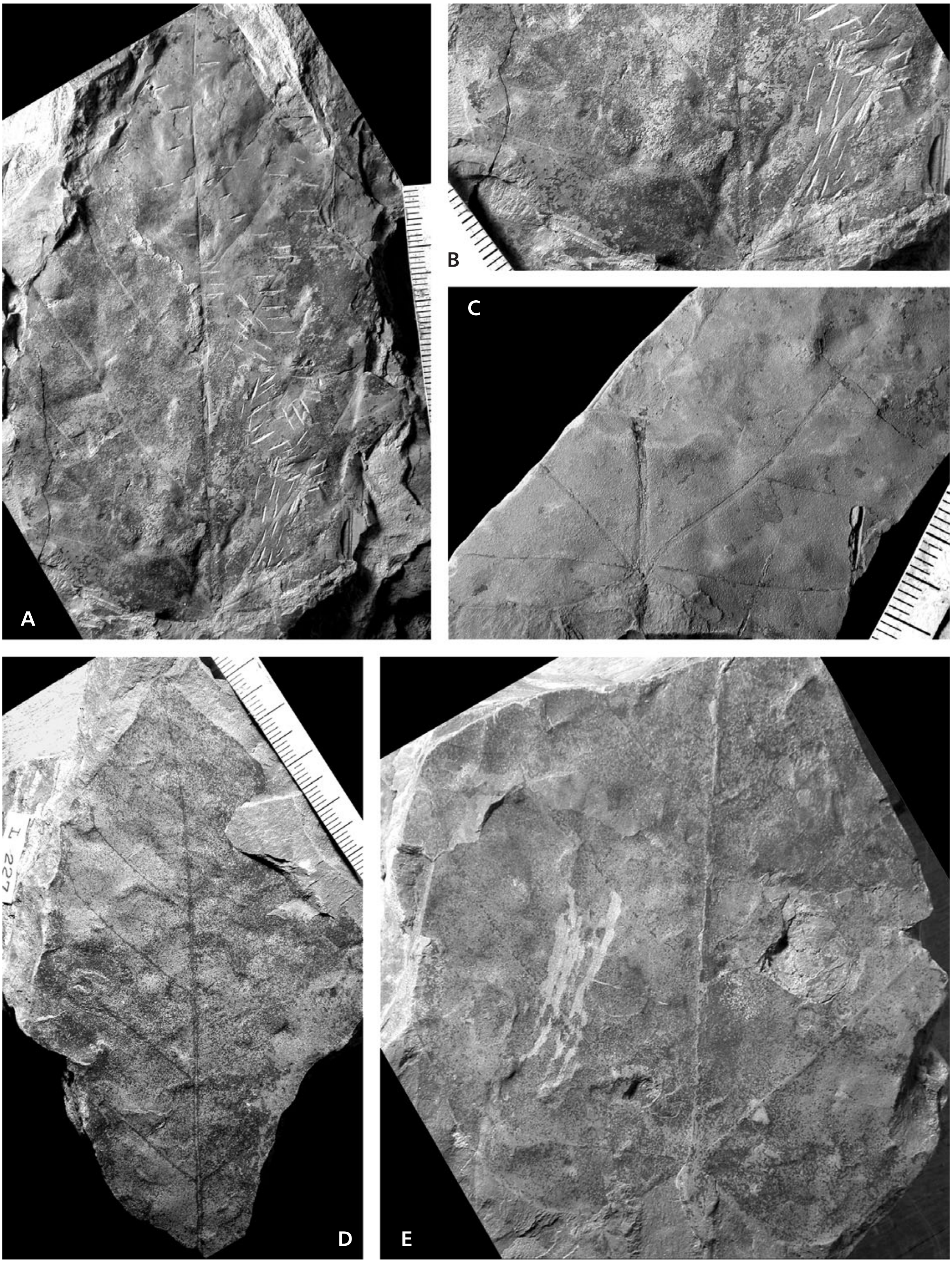


Figure 5. *Byttneriopsis steuerii* (Engelhardt) Kvaček & Wilde comb. nov., Lábatlan. • A – holotype of *Byttneria apiculata* É. Kovács (1959, fig. 4), MAFI Bk 3485 (L 28), × 1. • B – detail of leaf base from the previous specimen, × 1.5. • C – incomplete subcordate leaf base, MAFI Bk 3476 (L 23) × 1.5. • D – incomplete leaf showing leaf apex, MAFI Bk 3588 (L 227), × 1. • E – incomplete leaf with cordate base re-illustrated from Kovács (1959, fig. 6), MAFI Bk 3593 (L 14), × 1.3.

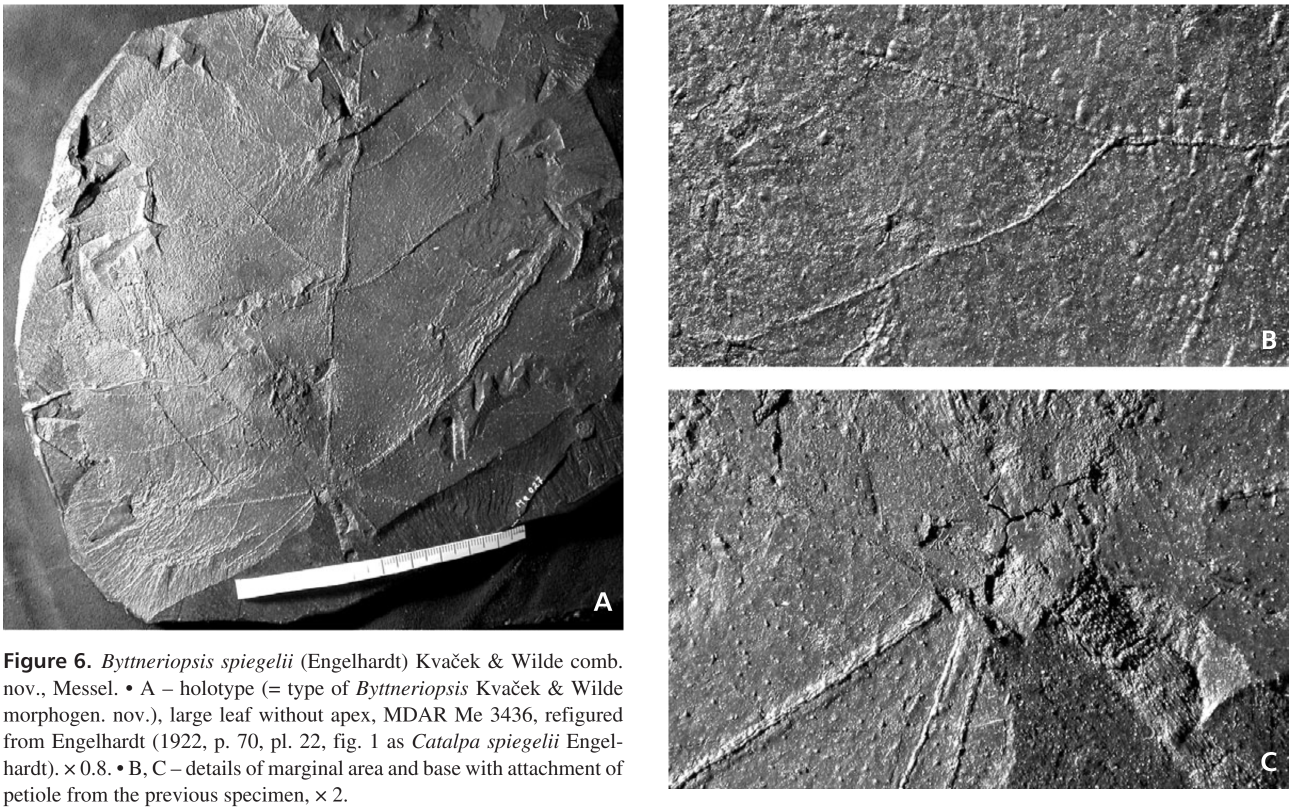


Figure 6. *Byttneriopsis spiegelii* (Engelhardt) Kvaček & Wilde comb. nov., Messel. • A – holotype (= type of *Byttneriopsis* Kvaček & Wilde morphogen. nov.), large leaf without apex, MDAR Me 3436, refigured from Engelhardt (1922, p. 70, pl. 22, fig. 1 as *Catalpa spiegelii* Engelhardt). × 0.8. • B, C – details of marginal area and base with attachment of petiole from the previous specimen, × 2.

slightly convex, distal end of wing rounded; venation-like structure on the straight margin.

Holotype designated here. – SM.B Me 5587, illustrated in Fig. 9A – Middle Eocene, Messel.

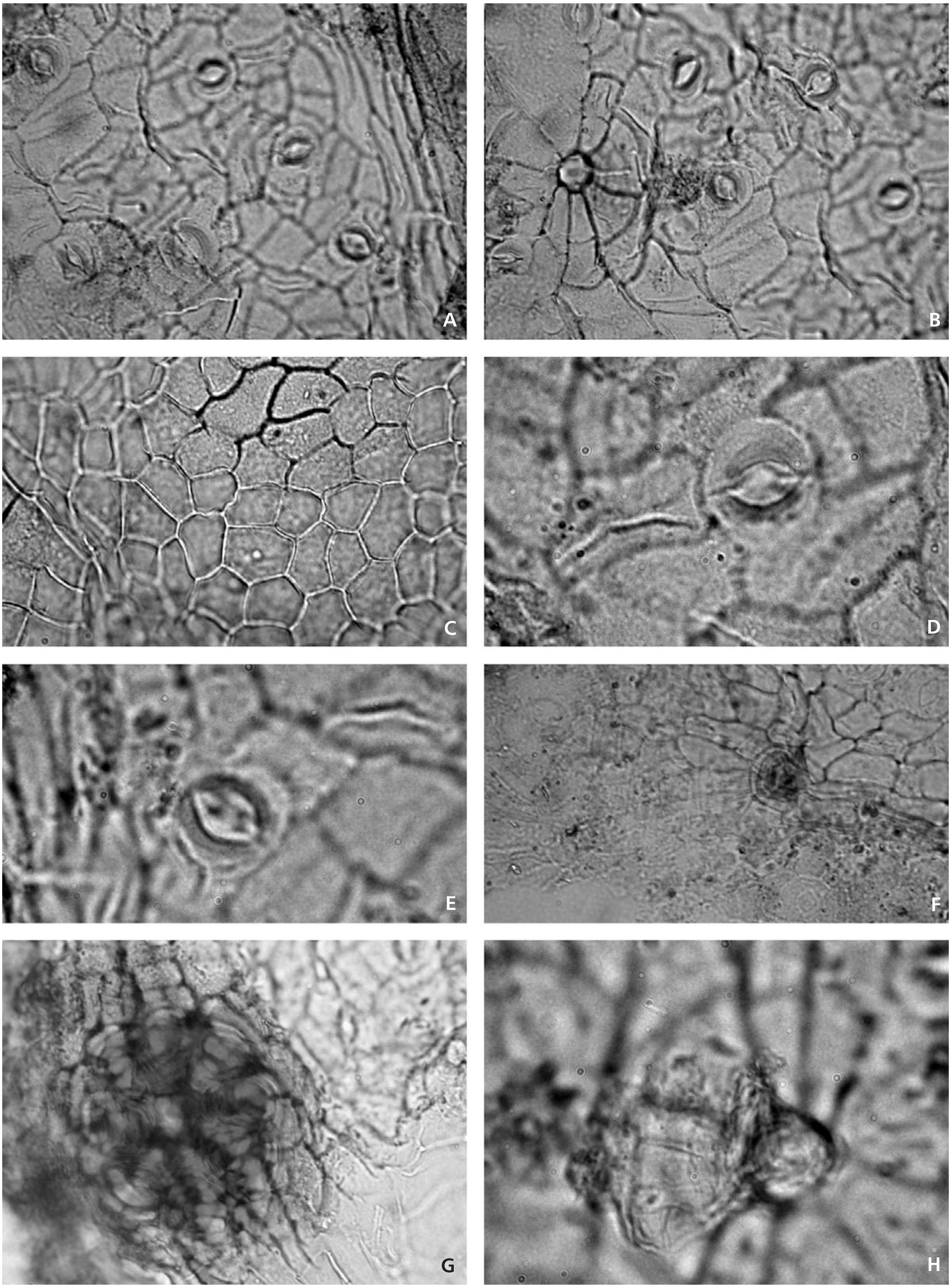
Etymology. – The epithet is established in recognition of Mrs. Éva Kovács, a Hungarian palaeobotanist and the first discoverer of such fossils in the Eocene of Hungary.

Description. – Several morphotypes connected with transitions can be recognized and assigned here to the same species, expressing, in our opinion, merely different stages of maturation:

Cedrelospermum sp. type I *sensu* Kovács (1959, p. 140, fig. 7 – Lábatlan, MAFI BK 3460/5/a) (Fig. 8C, F) and most of the material from Messel and Kučlín represent fully mature seeds with a robust seed body, sometimes truncate or with a more acute base, *ca* 9 mm long and 4–6 mm high. The wing is almost parallel-sided, slightly narrowed towards the end, 22 to 28 mm long. The dorsal side of the wing is straight, slightly thickened and indistinctly deflected behind the seed body; the ventral side is also straight. Under high magnification, the wing appears partly faintly striated due to strands forming the surface tissue. The specimens from Lábatlan designated as *Cedrelospermum* sp. type II *sensu* Kovács (1959, p. 140, fig. 8, MAFI BK 3526/L 107 and other not figured material BK 3487/L26, 24) are smaller than the previous morphotype I with the wing 16 mm long, the dorsal side straight or slightly bent and the ventral side straight (Fig. 9D, E). A specimen from Messel (SM. B Me 4115) with the seed body narrowed and at the base partly beak-like (Fig. 8B), finely pitted on the surface, 9 mm long and 4 mm tall, attached obliquely to the 22 mm long wing, may belong to the same morphotype because of variation in winged seeds being common in the Malvaceae due to variable position in the fruit capsule (*e.g.* in *Pterospermum* – Fig. 9K, L).

Additional material studied. – Messel – SM.B ME 2181, 4115, 7224, 8380 (part and counterpart) 16455 17019, 16836, 17836, 17020, 19885, 19950, 20181, 21620, 21622, 21809; Lábatlan – MÁFI BK 3460, BK 3487, BK 3526; Kučlín, Dead Hill (Mrtvý vrch, Totenberg) – DB KsMr01.

Figure 7. *Byttneriopsis steuerii* (Engelhardt) Kvaček & Wilde comb. nov., cuticular structures of specimen SM.B Me 908 shown in Fig. 4A from Messel. • A – abaxial cuticle showing incompletely cyclocytic stomata. • B – abaxial cuticle showing incompletely cyclocytic stomata and base of a glandular trichome. • C – adaxial cuticle with straight to curved anticlines, D, E – detail of stomata. • F – small compound trichome base, G – massive compound trichome base of stellate trichome. • H – glandular barrel-shaped trichome on abaxial cuticle. All figures × 600 except D, E, and H × 1500.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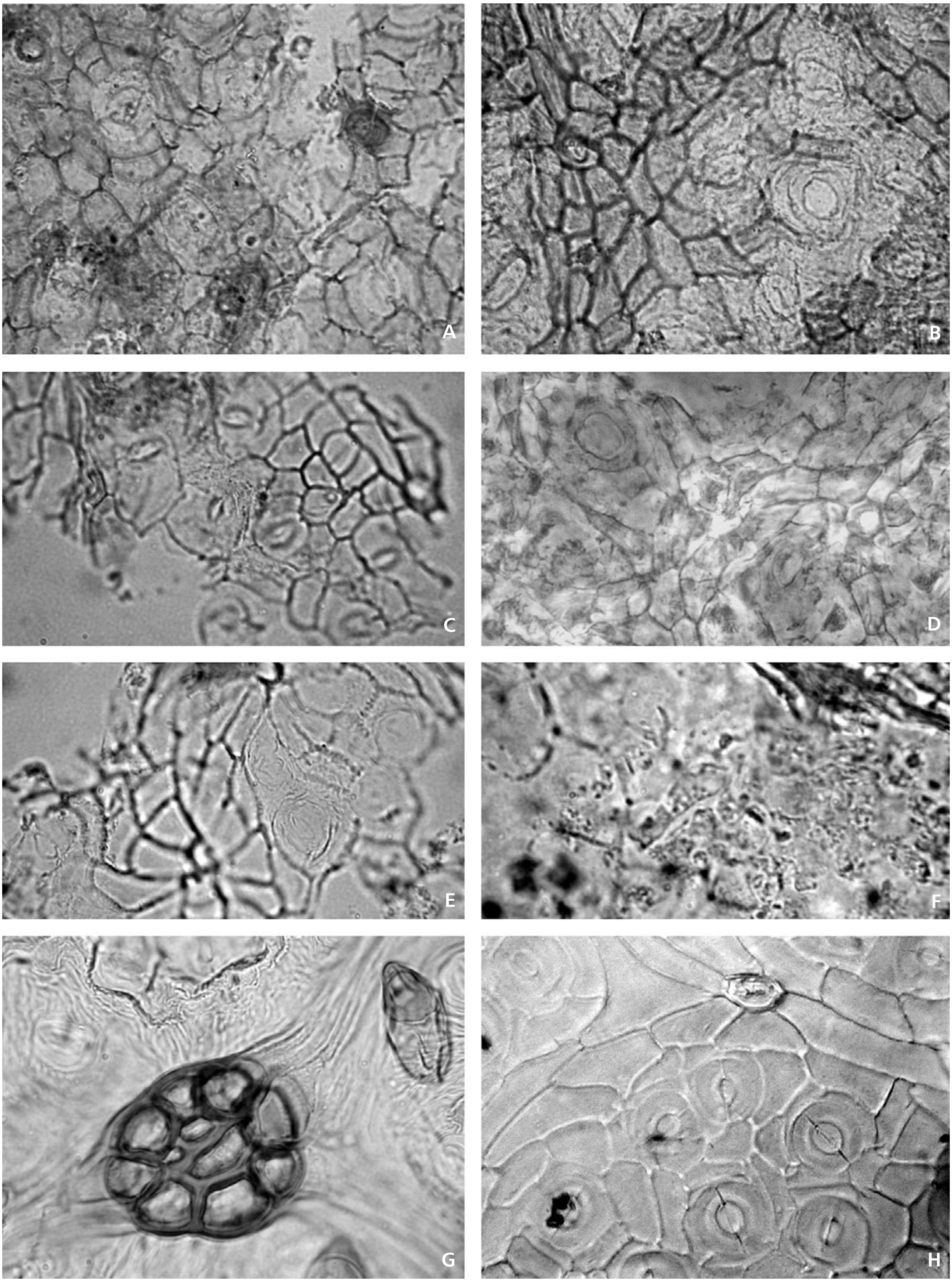
Remarks. – This type of seeds accompanies the foliage of *Byttneriopsis daphnogenes* as well as *B. steuerii* at all the three localities studied. Such winged seeds are known in several genera of the Malvaceae *s.l.*, *e.g.*, *Pterospermum*, *Eriolaena*, *Reevesia*, *Nesogordonia* Baill, *etc*. An assignment of such seeds to *Cedrelospermum* Saporta as suggested by Kovács (1959) is now inappropriate since Manchester (1987) re-defined this genus to include only fruits of the samara type belonging to an extinct member of the Ulmaceae (type *Cedrelospermum aquense* (Saporta) Saporta, Late Oligocene, Aix-en-Provence). The previously widely adopted morphogenus *Embothrites* Unger (type *Embothrites borealis* Unger, 1850a, p. 428, 1850b, p. 171, *partim*, pl. 21, figs 11, 12 (non fig. 10 – leaf), Upper Eocene in Socka – see Manchester 1987, 1989) is now restricted to those winged seeds with a sub-circular seed body attached directly by a neck to the elliptical wing, which is about twice as long as the seed body and shows fine dichotomous venation (Manchester 1987, type in pl. 3, figs 3, 4).

The seeds of *Gordonia* Ellis., both fossil and extant (Grote & Dilcher 1992), appear similar to our fossils, but differ in the oblique orientation of the seed body towards the apical wing and the position of the hilum and the dorsal part. A similar type of fossil winged seeds was described within the morphogenus *Saportaspermum* as *S. occidentale* Meyer & Manchester (1997), which is characterized by an ovate to elliptical seed body orientated obliquely (at an angle of 40°) to the lateral elongate wing, without apparent veins. The position of the hilum has not been indicated. The seed body continues into the dorsal part of the wing by a distinct tapered raphe, without any indentation, and there is also no distal notch, contrary to *Cedrelospermum* fruits. The seeds from Messel may be assigned to *Saportaspermum* (Collinson *et al.*, work in progress) and we agree with this generic assignment. The *Saportaspermum* type of seed was widespread from the Oligocene to the Miocene of Europe (*e.g.*, Hably *et al.* 2000) and has usually been assigned to *Embothrium salicinum* (Ettingshausen) Heer (*e.g.*, Unger 1867, Bůžek *et al.* 1976). But the latter name is not suitable being based primarily on the leaf fossils from Häring, Austria (*Santalum salicinum* Ettingshausen 1853). Saporta (1889) recognized such a seed type as belonging to the *Cedrelospermum* group *Aneuroptera*, *e.g. C. tenerum* Saporta, *C. abietinum* Saporta *etc*. (Saporta 1889, pl. 18, fig. 5) and stressed the difficulties in delimiting affinities of such fossil winged seeds in general.

In addition to *Cedrela* P. Br., which is also known in the fossil state (*e.g.* Meyer & Manchester 1987, Oligocene of the John Day Formation, Oregon), generally similar winged seeds without distinct veins in the wing (*Cedrela*-like *sensu* Manchester) are produced by plants of very varied affinities. According to Manchester (personal communication June 2004), such seeds are common in the Malvaceae (*Reevesia*, *Pterospermum*, *etc*. – Kvaček 2006), but also occur in the Celastraceae R. Br. (*Kokoona* Thw. *etc*.), Ericaceae Juss. (*Craibiodendron* W.W. Smith), Eucryphiaceae Endl. (*Eucryphia* Cav.), Flacourtiaceae DC. (*Carrierea* Franch.), Altingiaceae Lindl. (*Liquidambar* L.), Hippocrateaceae Juss. (*Campylostemon* Welw., *etc*.), Ixonanthaceae Klotzsch (*Ixonanthes* Jack), Lythraceae Jaume St-Hil. (*Lagerstroemia* L.), Meliaceae Juss. (*Toona* M. Roem., *Swietenia* Jacq., *etc*.), Oleaceae Hoffmgg. & Link. (*Schrebera* Roxb.), Onagraceae Juss. (*Eucharidium* Fisch. & Mey.), Proteaceae Juss. (*Embothrium* J.R. & G. Forst.), Ptaeroxylaceae Sonder (*Cedrelopsis* Baill., *etc*.), Rosaceae Juss. (*Kageneckia* Ruiz & Pav.), Rutaceae Juss. (*Chloroxylon* DC.), Sapindaceae (*Diplokeleba* N.E. Br.), Theaceae Mirb. (*Gordonia* Ellis), and Vochysiaceae A. St-Hil. (*Vochysia* Aubl.). A detailed comparative study is beyond the scope of the present paper and we are adding information on the seed fossils mainly for future consideration. From the preliminary survey of winged seeds in several genera of Malvaceae, such as *Nesogordonia* (Fig. 9L), *Helmiopsis* H. Perrier, *Helmiopsiella* Arènes, *Eriolaena* (Fig. 9J), and *Reevesia* (Fig. 9M), those of *Pterospermum* (Fig. 9I, K, L) best match our fossils. Particularly, we have observed similar variation of the seed shape in fully ripened seeds (rounded forms) and unripe or aborted seeds (awl-shaped base) in one, and the same fruit in *Pterospermum.* The flattened form of the seed and the wing of *Saportaspermum kovacsiae* suggests that it should adhere flat to a solid wall (?capsule valve), as in *Pterospermum*, rather than packed in a broader locule with irregularities in the form, as in *Gordoniopsis* Grote & Dilcher (1992). Unfortunately, the corresponding fruit remains, capsules or capsule valves that would reveal further traits, such as attachment and orientation of the seeds have not been recovered so far from Messel or any other sites.

A very similar type of seed compression has been de-

Figure 8. Cuticular structures of various fossil and living Malvaceae. • A – *Byttneriopsis daphnogenes* (Ettingshausen) Kvaček & Wilde, comb. nov., abaxial cuticle with dense glandular trichome bases, Messel, SM.B Me 1595/1. • B – *Byttneriopsis daphnogenes* (Ettingshausen) Kvaček & Wilde, comb. nov., abaxial cuticle of specimen shown in Fig. 2E with granular striate surface, Messel, SM.B Me 1452/1. • C – *Byttneriopsis steuerii* (Engelhardt) Kvaček & Wilde comb. nov., abaxial cuticle of specimen shown in Fig. 3A with single glandular trichome base, Messel, SM.B Me 1428/1. • D – *Byttneriopsis steuerii* (Engelhardt) Kvaček & Wilde comb. nov., abaxial cuticle of the holotype shown in Fig. 4C, D, Messel, phase contrast light, MDAR Me 1637/1. • E – *Byttneriopsis spiegelii* (Engelhardt) Kvaček & Wilde comb. nov., abaxial cuticle of the holotype shown in Fig. 6A, Messel, MDAR Me 3436/1. • F – adaxial cuticle of the same specimen. • G – *Eriolaena wallichii* DC., abaxial cuticle showing massive base of a stellate trichome and a complete glandular barrel-shaped trichome, India Orientalis, Hooker & Thomson 1859 (P). • H – *Burretiodendron brilletii* Kostermans, abaxial cuticle with cyclocytic stomata and a glandular trichome base, Tonkin, Brillet 19 (P). All figures × 600.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scribed from the Early Oligocene Seifhennersdorf site as *Saportaspermum dieteri* Walther & Kvaček (2007). We hesitate to merge our material with this morphospecies on account of subtle differences in gross morphology (beak-like and strongly thickened seed bodies, and the only slightly bent form of the wing in our material) and very different associated foliage at the Eocene sites of Messel, Kučlín and Lábatlan versus that of the Oligocene flora of Seifhennersdorf.

Comparison with the living Malvaceae *s.l.*

Foliage forms similar to *Byttneriopsis* are produced by plants belonging to many diverse groups. The arguments why the studied foliage is in our opinion of malvalean affinity are mainly based on epidermal anatomy, although our search for the nearest living relatives of *Byttneriopsis* has relied in fact on composite characteristics of leaf architecture, epidermal anatomy and co-occurring winged seeds. The type of indumentum described above, namely the glandular trichomes and complex thickly cutinized trichome bases (Figs 6G, H, 7G), rules out many families with convergent leaf morphology, *e.g. Matudaea* Lundell (Hamamelidaceae), *Sloanea* L. (Elaeocarpaceae), *Cinnamomum* Schaefer and other lauroids and *Ficus* (Moraceae) with partly triveined leaves, when considering only groups occurring in the European Palaeogene.

Gross morphology of foliage offers hardly any differentiating characters to elucidate more precisely the generic affinities within the extant Malvaceae *s.l.* Similar entire-margined non-lobate leaf forms with symmetrical actinodromous venation occur generally in the Malvaceae *s.l.* We may list several genera, which contain species bearing foliage of similar forms. The venation may not be stable throughout a genus (*e.g. Reevesia* with both purely actinodromous and pinnate venation). We have excluded from our comparison representatives of mostly dentate foliage with chartaceous texture, such as *Tilia* L., *Sparmannia* L.f., *Eriolaena* and many others. Entire-margined leaf forms with firm texture similar to *Byttneriopsis* occur *e.g.* in the Byttnerioideae Burrett, Brownlowioideae Burret, Helicteroideae (Schott & Endl.) Meisn. and Dombeyoideae Beilschm. But some of these are distinguished by asymmetrical or even subpeltate leaf bases.

The occurrence of glabrate leaves in the Malvaceae, as in *Byttneriopsis,* is rare. Foliage of most members is pubescent with stellate trichomes to a varied degree of density and trichome types, at least on the undersurface of the leaf. Our limited collection of cuticular preparations does not contain samples, which would fully match the epidermal pattern of the above described morphospecies of *Byttneriopsis*. We have attempted to follow indications offered by co-occurrences of winged seeds obviously matching those of *Pterospermum*, *Reevesia* and others without success. *Pterospermum*, *Eriolaena* (Fig. 8G) and several other genera (*Brownlowia* Roxb., *Schoutenia* Korth., *Hildegardia* Schott & Endl., *Melhania* Forsk.) are typical of massive, strongly cutinized, and sometimes elongate, trichome bases as in *Byttneriopsis*, which bear stellate trichomes often densely dispersed on the abaxial leaf side. Other genera have a varyingly dense indumentum of sessile stellate trichomes (*Reevesia*, *Hainania* Merr., *Pentace* Hassk., *Colona* Cav., *Helicteres* L.) or consisting of single, paired or rare fasciculate trichomes (*Byttneria* Loefl., *Dombeya* Cav., *Craigia*, partly *Sterculia* L.). We have found only a few cases of glabrate abaxial epidermis with cyclocytic stomata resembling our material, such as *Burretiodendron* Rehder – Fig. 8H (*B. esquirollii* Rehder with peltate trichomes), *Excentrodendron* Chang & Miau, *Pterygota* Schott & Endl., and *Scaphium* Endl. Some species of *Reevesia* may resemble *Byttneriopsis* but differ in brachyparacytic stomata. Concluding this brief survey, we may state that *Byttneropsis* probably represents foliage of an extinct member of the Malvaceae *s.l.* sharing characters of several extant genera.

Paleoecology of the studied Eocene Malvaceae

According to the relatively thin cuticles of the material from Messel, the plants which produced *Byttneriopsis* foliage should have been deciduous. Deciduousness is not unusual even in warmer climates and may depend on the periodicity of precipitation (available humidity) during the year. However, thin cuticles with very similar patterns to *Byttneriopsis* are also produced by some evergreen Malvaceae, such as *Burretiodendron* and *Excentrodendron.* The possible analogues of these plants grow today under subtropical to paratropical conditions in East Asia and Central America (*Reevesia*, *Pterospermum*, *Eriolaena*). The fossil

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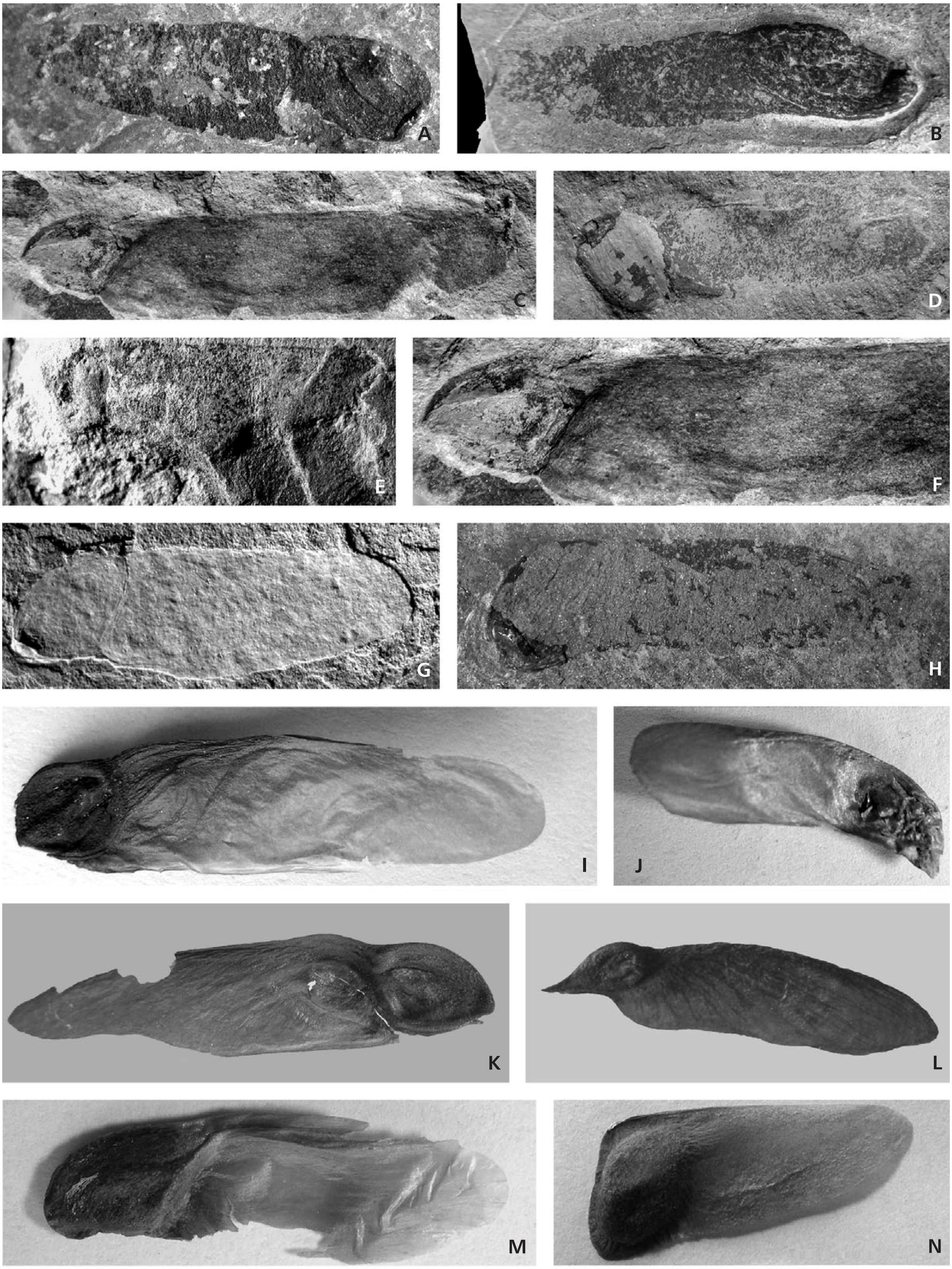
Figure 9. *Cedrelospermum kovaciae* Kvaček & Wilde sp. nov. (A–H) and seeds of living Malvaceae for comparison (I–M). • A – holotype, Messel, SM.B Me 5587. • B – anomalous seed with narrowed body, Messel, SM.B Me 4995. • C – refigured specimen of *Cedrelospermum* sp. 1 *sensu* Kovács (1959, fig. 7), Lábatlan, MAFI Bk 3460. • D – refigured specimen of *Cedrelospermum* sp. 2 *sensu* Kovács (1959, fig. 8), Lábatlan, MAFI Bk 3526. • E – poorly preserved seed, Lábatlan, MAFI Bk 3487. • F – enlarged seed part of *Cedrelospermum* sp. 1 *sensu* Kovács (1959, fig. 7), Lábatlan, MAFI Bk 3460. • G – seed impression, Mrtvý vrch at Kučlín, DB KsMr01. • H – counterimpression of carbonized seed, Messel, SM.B Me 8383b. • I – *Pterospermum levinei* Merr., Hainan, Fung 20331 (P). • J – *Eriolaena candollii* Wall., Thailand, van Beusecome & Phengklai 2337 (P). • K – *Pterospermum pierii* Hance, two unequally sized seeds from the same capsule, Thailand, Pierre 3776 (P). • L – *Reevesia macrocarpa* Li, Tonkin, Tsang 30473 (P). • M – *Nesogordonia stylosa* Perrier, Madagaskar, Capuron 247455 F (P). All figures × 3 except F × 4.5.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representatives were certainly zonal woody in view of the associated assemblages at Messel, Kučlín and Lábatlan. Leaf physiognomic climate proxies (CLAMP analyses) are not available for any of the three sites because of a largely unknown spectrum of leaf dicot morphotypes. The co-existence approach (Mosbrugger & Utescher 1997), which is based on the autecology of comparable extant taxa, also fails in the case of such floras with extinct and also many unknown plants. The so far derived climatic conditions, based on general comparisons of the assemblages from Messel with living vegetation, led Wilde (2005) to suggest parallels with today's paratropical forests as defined by Wolfe (1979). However, the floras of Messel, Kučlín and Lábatlan differ in size categories of foliage, namely noto- to microphyllous, contrary to the paratropic forest vegetation with prevailing macrophyllous tress. Therefore, Kvaček (2010) proposed a new vegetation unit for such extinct European Palaeogene vegetation and called it "Mid-Latitude Broad-Leaved Notophyllous Evergreen Forest" characterized in general by dominating Lauraceae Juss., common and diversified Juglandaceae A. Rich. *ex* Kunth., Ulmaceae Mirb. (*Cedrelospermum* Saporta emend. Manchester), Leguminosae Juss., rare conifers (*Tetraclinis* Mast., partly azonal *Doliostrobus* Marion, *Cephalotaxus* Siebold & Zucc.) and various accessory exotic and extinct elements. Representatives of true tropical families do not dominate and the diversity of the flora is moderate. Before revision of the floras is completed, it is difficult to suggest more precise palaeoclimatic proxy data. It is certain that the climate under which *Byttneriopsis* thrived was frostless, warm and humid, approximately similar to that of the monsoon areas of East Asia, namely today's south and southeast China, northern Vietnam and Laos.

Acknowledgments

This work was supported by the Grant Agency of the Czech Republic (GAČR), project No. 205/08/0643 and the research scheme No MSM 002162085, Czech Republic to the first author. Thanks are due to the curators of the Paris Herbarium (P) who made the extant material of the Malvaceae accessible for study, and to Lilla Hably, Budapest, who organized the visit of the first author to Budapest. Jiří Kvaček, Prague, Zdeněk Dvořák, Bílina, and Barbara Meller, Vienna, all facilitated our study and the documentation of the plant fossils in the respective collections and are also acknowledged; Gabriele Gruber organized a short-term loan of type material from the Hessisches Landesmuseum Darmstadt. Co-operation with Grzegorz Worobiec, Kraków, in studying the leaf epidermal characters of the Malvaceae is much appreciated, as is technical and background support by Karin Schmidt and Martin Müller, Frankfurt am Main. Steven R. Manchester and Jakub Sakala provided helpful comments on the first version of the manuscript, and kindly reviewed and suggested improvements for the final form of our paper.

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