

DISTRIBUTION, TAPHONOMY AND PALAEOECOLOGY OF *ULMUS* L. IN THE HUNGARIAN EGERIAN

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The fossil remains, mainly leaves, of the genus *Ulmus* L. are one of the most characteristic elements of the Hungarian Upper Oligocene (Egerian). Systematic revision confirmed the occurrence of four elm species: *Ulmus pyramidalis* Goepp., *U. pseudopyramidalis* Z. Kvaček et Hably, *U. fischeri* Heer, and *Ulmus* cf. *minuta* Goepp. (= *U. plurinervia* Ung.). They are the earliest Arctotertiary taxa in the Hungarian Tertiary. *Ulmus pyramidalis* Goepp. is the most widespread elm in the Hungarian Egerian. The occurrence of the various *Ulmus* species at different Egerian localities was dependent on the prevailing palaeoecological conditions, with the sedimentological characteristics of the fossil locality also playing an important part.

Key words: *Ulmus*, Egerian, Hungary, palaeoecology, palaeogeography, taphonomy

INTRODUCTION

Several Upper Oligocene localities with plant remains have been studied taxonomically over the last 30–40 years by ANDREÁNSZKY (1966), HABLY (1982, 1988, 1989, 1990, 1993a, 1994), and KVAČEK and HABLY (1991). These Egerian floras have a very similar composition because they existed at the same time (*i.e.* Egerian, nannoplankton zone NP 24–25) and most of them represent remains of the zonal vegetation. From reconstruction of the vegetation it may be concluded that most of the species represent a palaeotropical, thermophilous element, except for a few temperate, Arctotertiary species, which represent an edaphic, intrazonal vegetation (HABLY 1993b).

The most important Arctotertiary element in these floras is the genus *Ulmus* L. Its presence is easily recognized, even in the sandy layers, in badly preserved floras (HABLY 2001). Almost 500 specimens of elm leaves were studied taxonomically from 9 Egerian localities, including the Egerian stratotype flora at the Eger-Wind brickyard. From the upper and middle strata in this locality about 200 undetermined and unpublished specimens were studied by the authors. The material is divided among the Hungarian Natural History Museum in Budapest (BP), the Mátra Museum at Gyöngyös (MM), and the Kúny Domokos Museum in Tata, Hungary.

DESCRIPTION OF THE *ULMUS* L. SPECIES FROM THE
EGER-WIND BRICKYARD*Ulmus pseudopyramidalis* Z. Kvaček et Hably
Figs 2–7

1991 *Ulmus pseudopyramidalis* Z. Kvaček et Hably: KVAČEK and HABLY, p. 56, Pl. 6, Fig. 1 (holotype)

1966 *Ulmus*, type I: ANDREÁNSZKY, p. 77, Figs 60–61

1966 *Ulmus*, type II: ANDREÁNSZKY, p. 77, Figs 62–63

1966 *Ulmus*, type III: ANDREÁNSZKY, p. 78, Figs 64–65

Material: BP 2001.1.1–BP 2001.6.1, BP 2001.8.1–BP 2001.10.1, BP 2001.12.1, BP 2001.13.1, BP 2001.15.1, BP 2001.16.1, BP 2001.18.1, BP 2001.20.1, BP 2001.23.1–BP 2001.28.1, BP 2001.32.1, BP 2001.34.1–BP 2001.36.1, BP 2001.40.1, BP 2001.43.1, BP 2001.45.1, BP 2001.48.1–BP 2001.50.1, BP 2001.52.1, BP 2001.53.1, BP 2001.58.1–BP 2001.61.1, BP 2001.63.1, BP 2001.66.1–BP 2001.70.1, BP 2001.72.1–BP 2001.76.1, BP 2001.78.1, BP 2001.80.1–BP 2001.82.1, BP 2001.84.1, BP 2001.87.1, BP 2001.88.1, BP 2001.92.1, BP 2001.94.1, BP 2001.98.1, BP 2001.101.1–BP 2001.103.1, BP 2001.139.1, BP 2001.142.1, BP 2001.149.1, BP 2001.150.1, BP 2001.154.1, BP 2001.157.1, MM 56.697.1, MM 56.762.1, MM 56.829.1, MM 61.785.1, MM 61.791.1, MM 65.744.1, MM 2001.1.1–MM 2001.7.1.

Description. Leaves mostly large, narrowly ovate, rarely narrow-elliptic, narrow-oblong or ovate, asymmetric, base mostly deeply cordate, asymmetric, rarely cuneate-rounded, apex acute or slightly attenuate. Length of leaves 6.2 to ca 13 cm, width (2.2) 3.2–6.0 cm, petiole 3–5 mm. Venation craspedodromous. Primary vein straight, stout. Secondary veins numerous, up to 18 (or even more) pairs in number, commonly arched throughout the leaf, not just in the apical part. Secondary veins occasionally forked, usually only in the cordate base, rarely in the mid-leaf. Secondary veins up to 1.0 cm apart. In the lower part of the leaf the secondaries diverge from the primary vein at an angle of 60–70° in the middle part at 50° and in the upper 40°. On some specimens there is visible branching of the secondaries at the leaf margin, but the third order venation is very poorly visible or not preserved at all. Because of the very poor state of preservation the leaf margin is incomplete. Most specimens possess only some marginal teeth which are distinct and simple (as in *Zelkova* leaves), particularly in the upper part of the leaf. In the middle part there is often small additional tooth on the lower side of each tooth.

Remarks. As stated by KVAČEK and HABLY (1991), the leaves of *U. pseudopyramidalis* “differ primarily in the strongly asymmetric leaf base, coarser teeth and partly also in their greater size”. They are most commonly large, with very characteristic arched secondary veins which diverge from the central vein at widely spaced intervals. The “*Zelkova*”-like teeth, sometimes with a small addi-

tional tooth, are also very characteristic for this species. *Ulmus pseudopyramidalis* is very similar to *U. drepanodonta* Grubov, described from the Oligocene of Kazakhstan (GRUBOV in KRISHTOFOVICH *et al.* 1956). Both have leaves of the same size, shape, venation and marginal characteristics with simple teeth furnished with a small additional tooth. The only difference is that the leaves of *U. pseudopyramidalis* Z. Kvaček et Hably have not additional lobes in the upper part.

Ulmus pyramidalis Goepf.

Figs 8–9, 10: 1–7

1855 *Ulmus pyramidalis* Goepf.: GOEPPERT, p. 29, Pl. 13, Fig. 11

1966 *Carpinus grandis* Ung.: ANDREÁNSZKY, p. 42, Figs 28–30

1991 *Ulmus pyramidalis* Goepf.: KVAČEK and HABLY, p. 56, Pl. 5, Fig. 1

Material: BP 2001.11.1, BP 2001.14.1, BP 2001.19.1, BP 2001.21.1, BP 2001.22.1, BP 2001.24.1, BP 2001.26.1, BP 2001.29.1, BP 2001.33.1, BP 2001.57.1, BP 2001.83.1, BP 2001.95.1, BP 151.1, MM 56.1407.1, MM 61.185.1, MM 61.186.1, MM 61.188.1–MM 61.191.1, MM 61.194.1, MM 61.195.1, MM 61.197.1–MM 61.199.1, MM 61.787.1, MM 61.788.2, MM 61.792.2, MM 61.941.1, MM 61.942.1, MM 62.640.1–MM 62.642.1, MM 62.647.1, MM 2001.9.1.

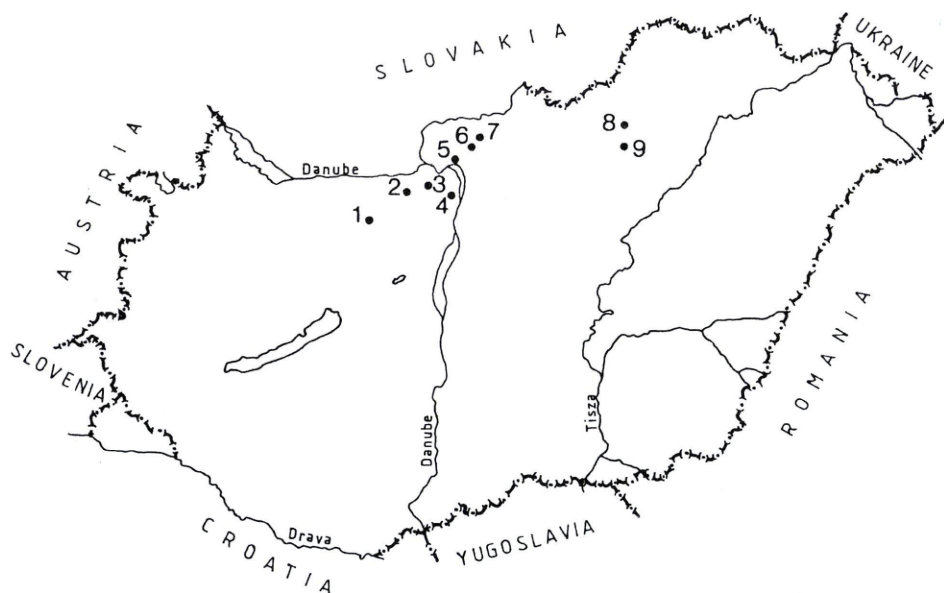


Fig. 1. Schematic map of the studied localities with the distribution of *Ulmus* L. 1. Vértesszőlős, 2. Nagysáp, 3. Keszthely, 4. Pomáz, 5. Verőcsemaros, 6. Rétság, 7. Pusztaberki, 8. Eger-Wind brickyard, 9. Andornaktálya.

Description. Leaves narrowly ovate, oblong or narrow-elliptic. Base rounded or cuneate, rarely asymmetric, apex acute or acuminate. Length of leaves 5.5 to 11.5 cm, mostly *ca* 10 cm, width 1.5–6.0 cm. Petiole 0.6–1.4 mm long. Venation craspedodromous. Primary vein straight, secondary veins 12 to 19 pairs, straight, 2–7 mm apart, closer together in the apical part of the leaf. The secondaries diverge from the central vein at an angle of *ca* 50° in the lower part of the leaf, 35–40° in the middle part. Forking of the secondary veins is rare and is present only on a few specimens, mostly in the lower part of the leaf. Leaf margin visible only on some specimens, simply serrate, particularly in the upper part of the leaf, rarely doubly serrate.

Remarks. The most characteristic features of the above-described fossil leaves are the close venation, particularly in the upper part of the leaf and the regular shape, mostly narrow-ovate or oblong. The whole leaf margin is not clearly visible because of poor preservation, but it should be noted, that simple teeth are visible in the upper part of the leaf.

Ulmus fischeri Heer

Fig. 10: 8, Fig. 11: 1–2, 4–5

1856 *Ulmus fischeri* Heer: HEER, p. 57, Pl. 79, Figs 1–3

1982 *Ulmus cf. fischeri* Heer: HABLY, p. 95, Pl. 2, Fig. 5, Pl. 7, Fig. 1

1991 *Ulmus fischeri* Heer: KVAČEK and HABLY, Pl. 5, Fig. 2

Material: BP 2001.7.1, BP 2001.8.1, BP 2001.9.1, BP 2001.30.1, BP 2001.31.1, BP 2001.39.1, BP 2001.41.1, BP 2001.64.1, MM 56.696.1.

Description. Leaves up to 11.0 cm long and 4 cm wide, asymmetric, with cordate base, apex unknown. Venation craspedodromous, secondary veins *ca* 16 pairs, slightly arched. Margin doubly serrate.

Remarks. Only some leaf fragments of this species of *Ulmus* are preserved. They are very similar to the leaves of *U. pseudopyramidalis*, but differ in the leaf margin which is doubly serrate.

Ulmus sp.

Fig. 12

1966 *Ulmus*-type IV: ANDREÁNSZKY, p. 78, Figs 66–67

1966 *Ulmus*-type V: ANDREÁNSZKY, p. 78, Fig. 68

Figured material: BP 2001.12.1, BP 2001.17.1, BP 2001.18.1, BP 2001.25.1, BP 2001.44.1, BP 2001.85.1.

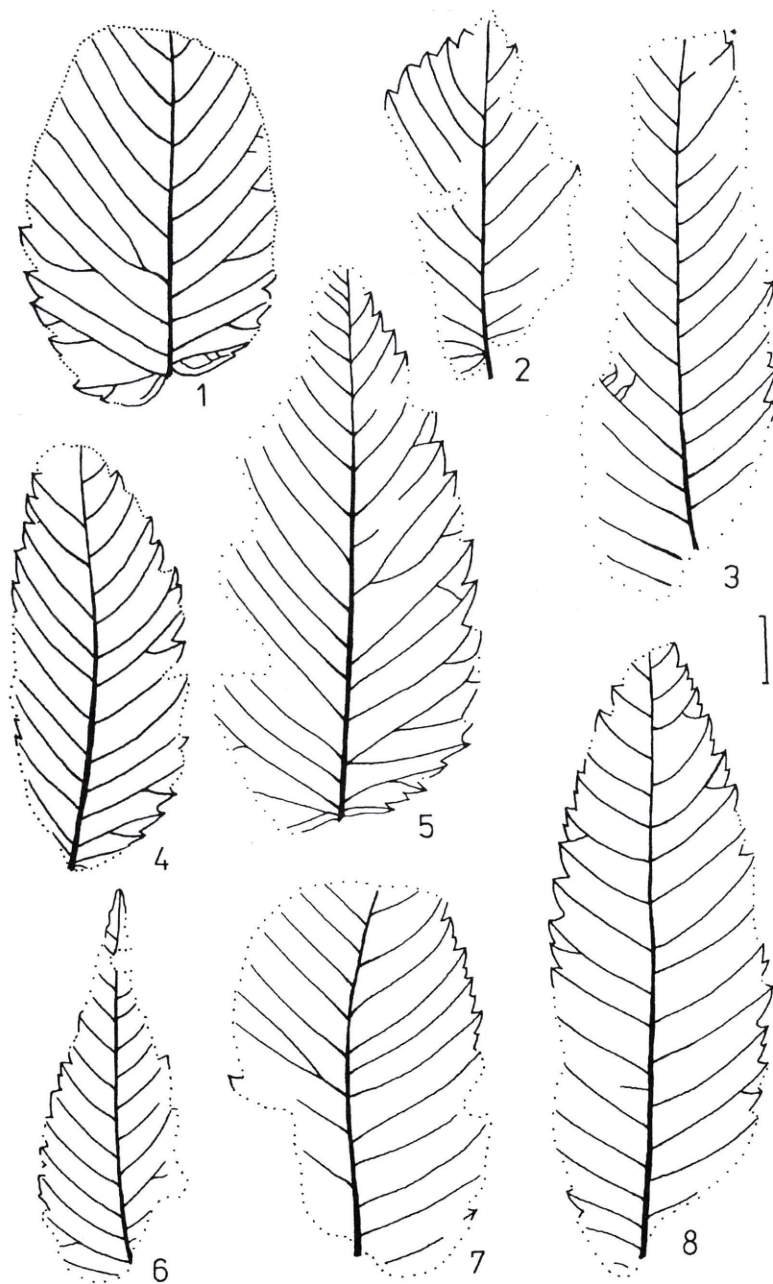


Fig. 2. *Ulmus pseudopyramidalis* Z. Kvaček et Hably (natural size). 1 = BP 2001.53.1; 2 = BP 2001.157.1; 3 = BP 2001.18.1; 4 = BP 2001.150.1; 5 = BP 2001.73.1; 6 = BP 2001.23.1; 7 = BP 2001.69.1; 8 = BP 2001.139.1.

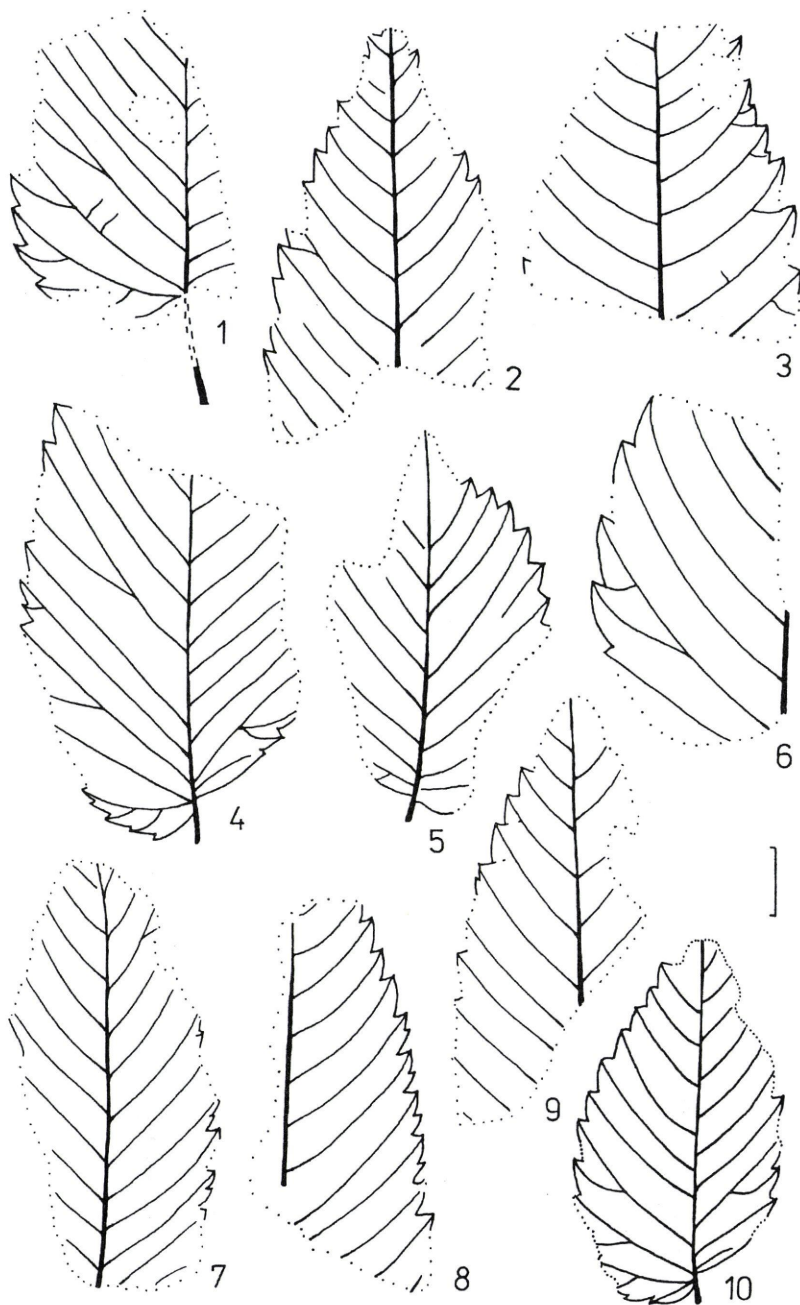


Fig. 3. *Ulmus pseudopyramidalis* Z. Kvaček et Hably (natural size). 1 = BP 2001.48.1; 2 = BP 2001.4.1; 3 = BP 2001.6.1; 4 = BP 2001.84.1; 5 = BP 2001.154.1; 6 = BP 2001.40.1; 7 = BP 2001.103.1; 8 = BP 2001.67.1; 9 = BP 2001.12.1; 10 = BP 2001.72.1.

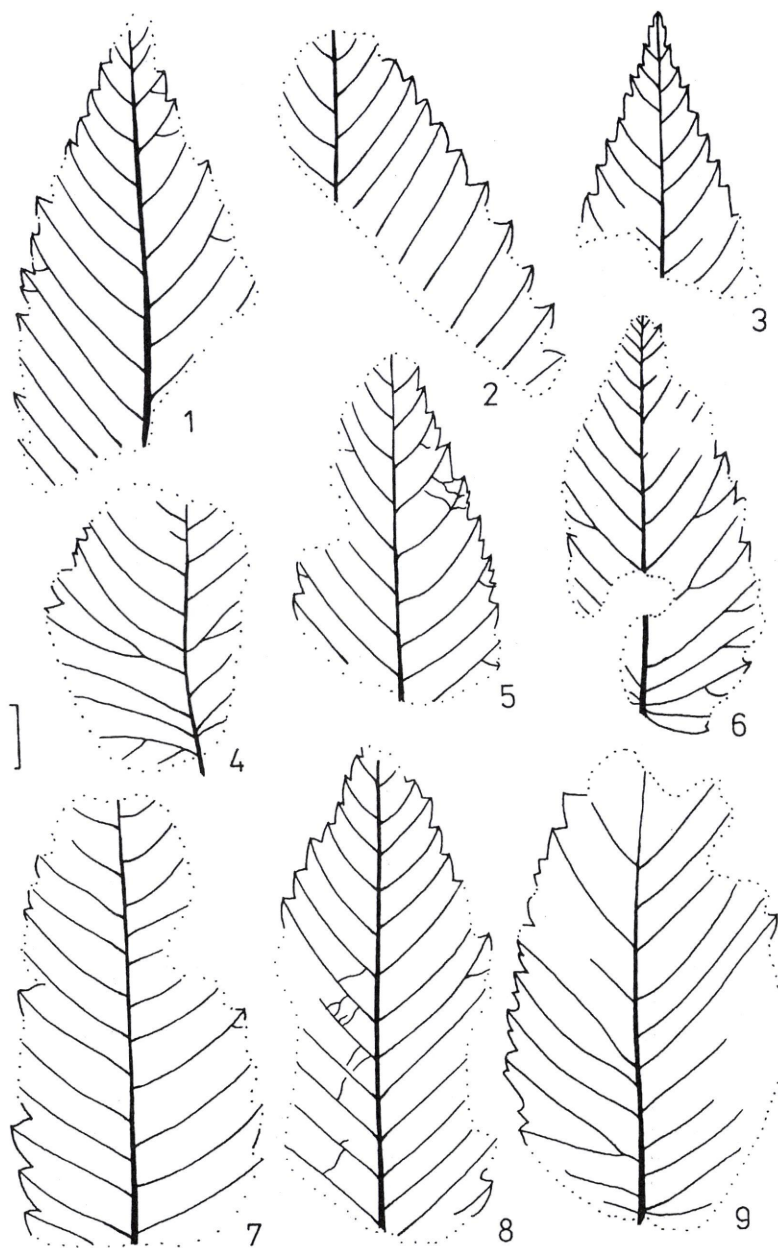


Fig. 4. *Ulmus pseudopyramidalis* Z. Kvaček et Hably (natural size). 1 = BP 2001.70.1; 2 = BP 2001.63.1; 3 = BP 2001.15.1; 4 = BP 2001.34.1; 5 = BP 2001.102.1; 6 = BP 2001.80.1; 7 = BP 2001.59.1; 8 = BP 2001.82.1; 9 = BP 2001.3.1.

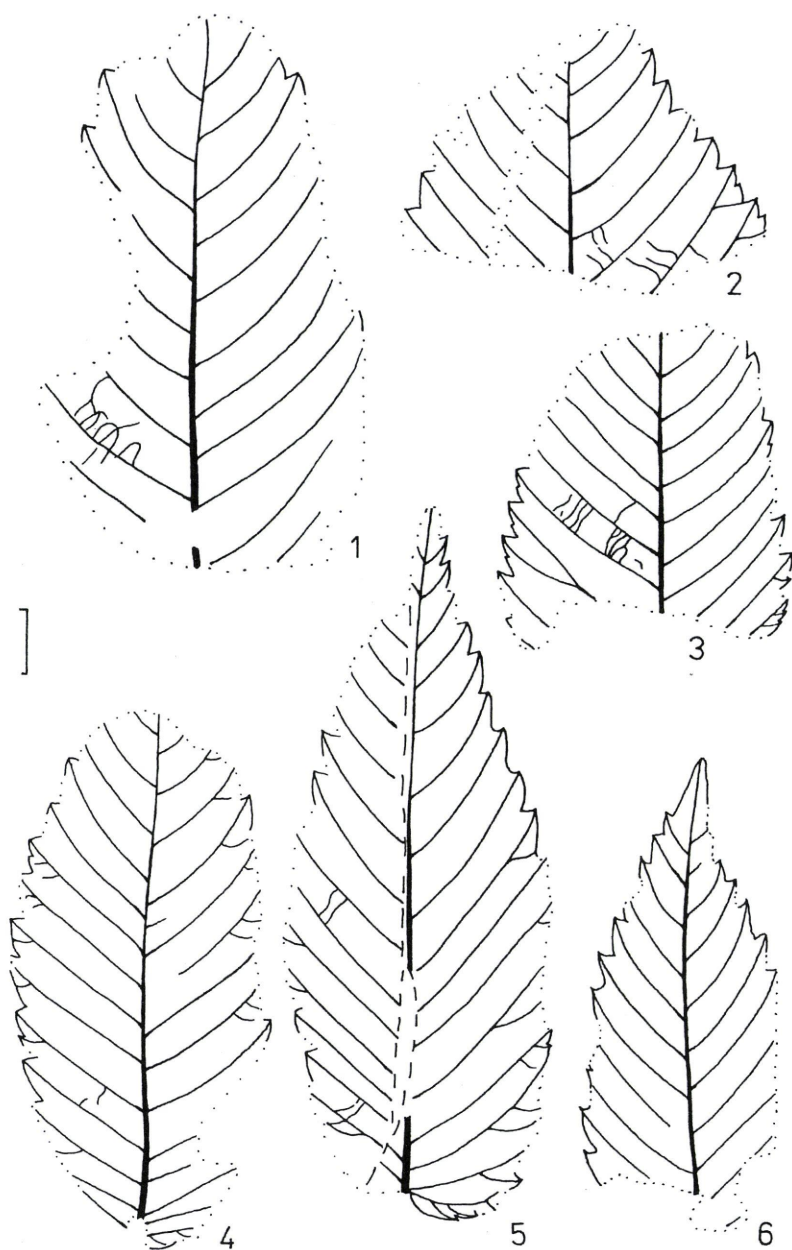


Fig. 5. *Ulmus pseudopyramidalis* Z. Kvaček et Hably (natural size). 1 = BP 2001.43.1; 2 = BP 2001.142.1; 3 = BP 2001.52.1; 4 = BP 2001.10.1; 5 = BP 2001.5.1; 6 = BP 2001.20.1.

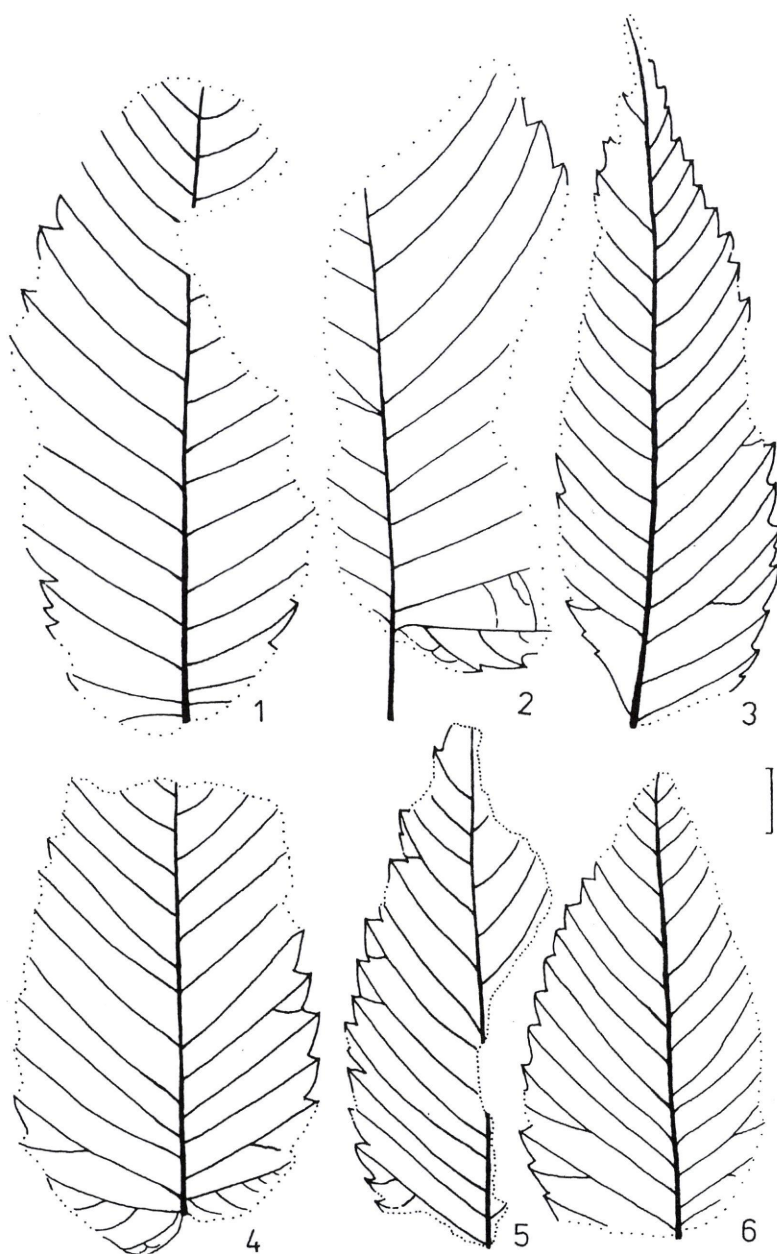


Fig. 6. *Ulmus pseudopyramidalis* Z. Kvaček et Hably (natural size). 1 = BP 2001.8.1; 2 = 2001.36.1; 3 = BP 2001.13.1; 4 = BP 2001.35.1; 5 = BP 2001.60.1; 6 = BP 2001.92.1.

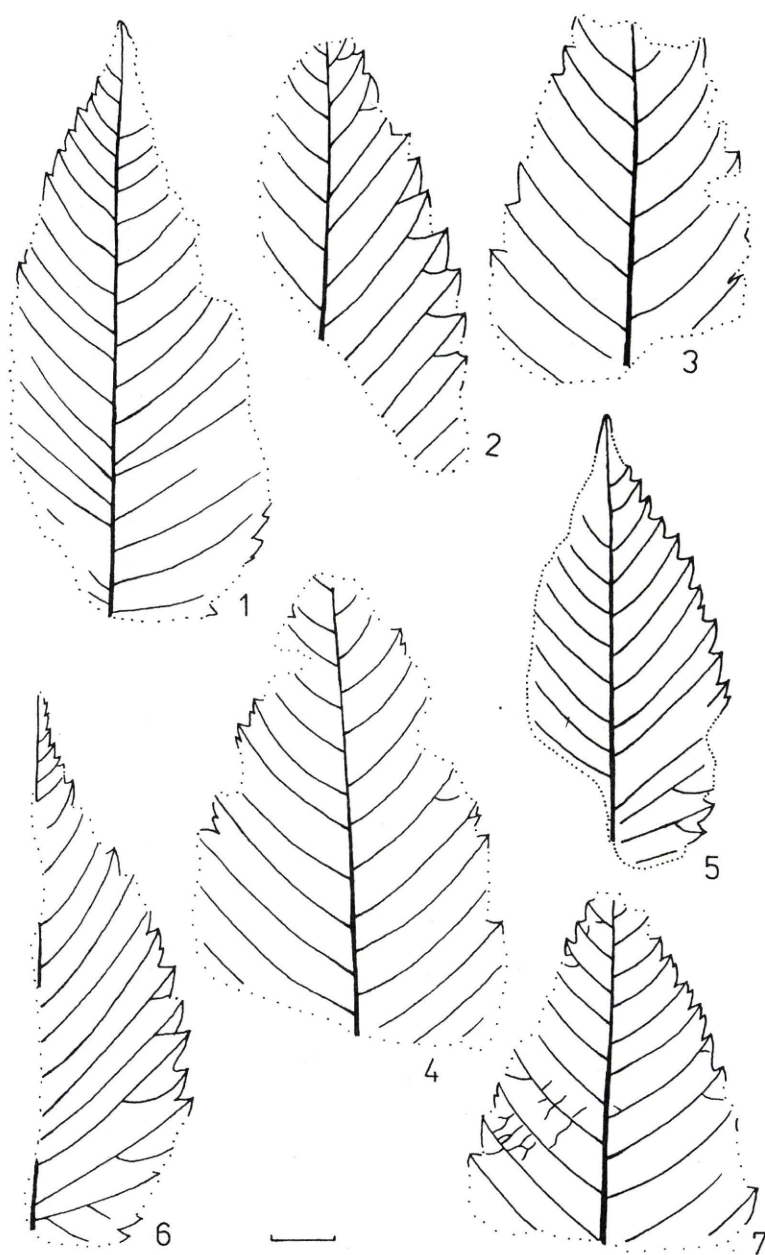


Fig. 7. *Ulmus pseudopyramidalis* Z. Kvaček et Hably (natural size). 1 = MM 2001.1.1; 2 = BP 2001.94.1; 3 = BP 2001.149.1; 4 = BP 2001.49.1; 5 = BP 2001.3.1; 6 = BP 2001.76.1; 7 = BP 2001.78.1.

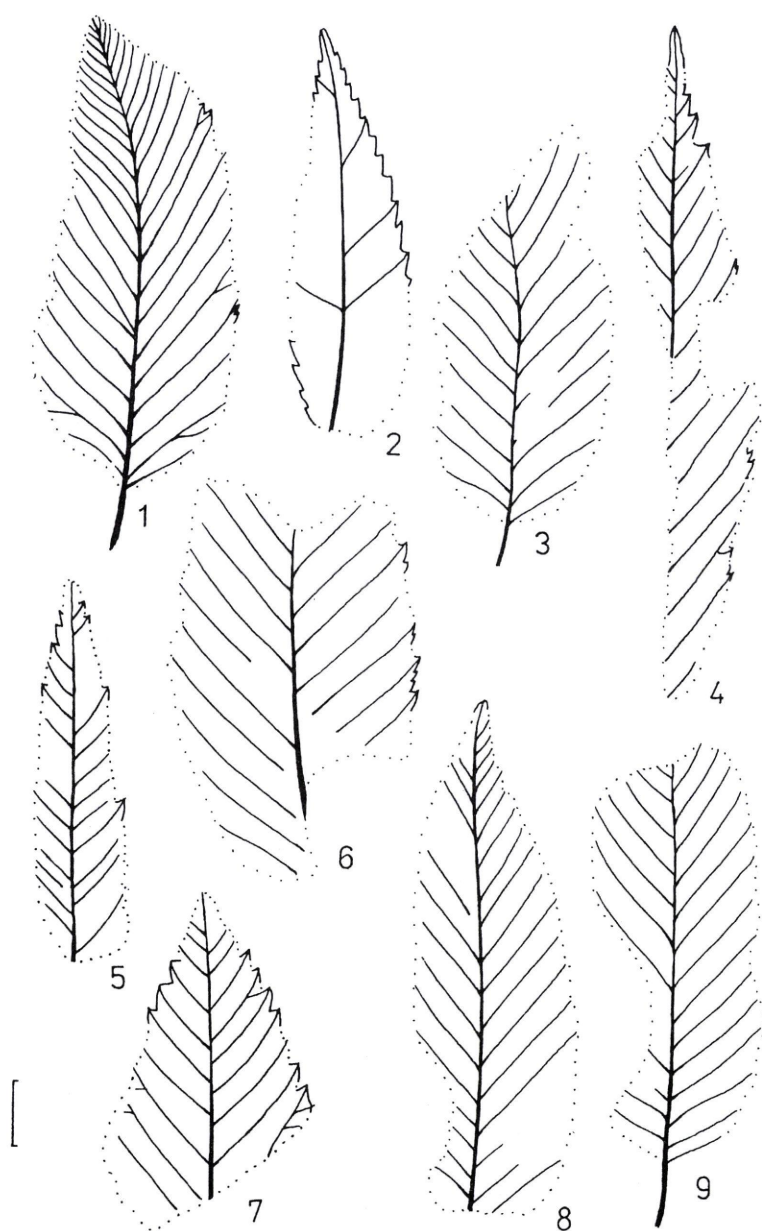


Fig. 8. *Ulmus pyramidalis* Goepp. (natural size). 1 = MM 61.190.1; (as *Carpinus grandis* Ung., ANDREÁNSZKY 1966, Fig. 30); 2 = BP 2001.14.1; 3 = MM 61.941.1; 4 = BP 2001.21.1; 5 = BP 2001.19.1; 6 = MM 61.942.1; 7 = BP 2001.95.1; 8 = MM 61.199.1; 9 = MM 61.792.2.

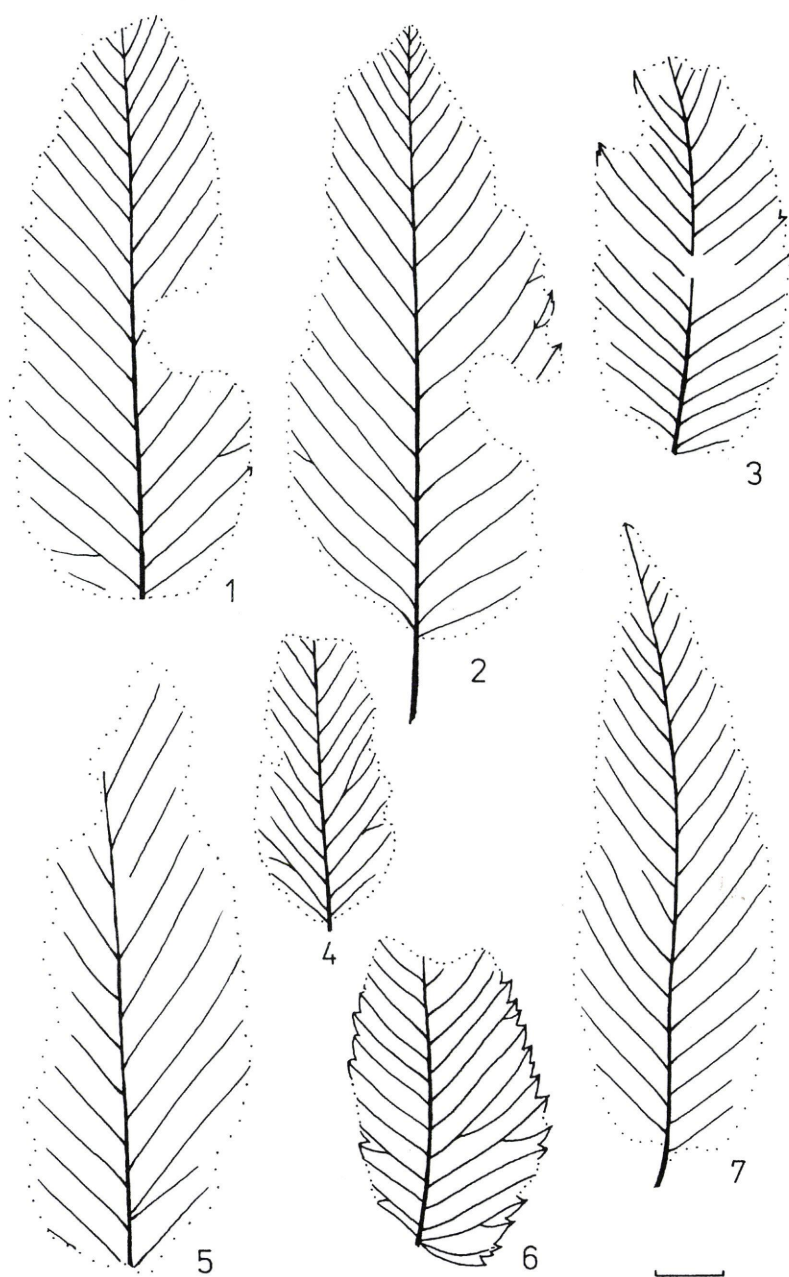


Fig. 9. *Ulmus pyramidalis* Goepp. (natural size). 1 = MM 62.641.1; 2 = MM 61.788.2; 3 = MM 62.640.1; 4 = MM 61.185.1; 5 = MM 61.197.1; 6 = BP 2001.33.1; 7 = MM 62.642.1.

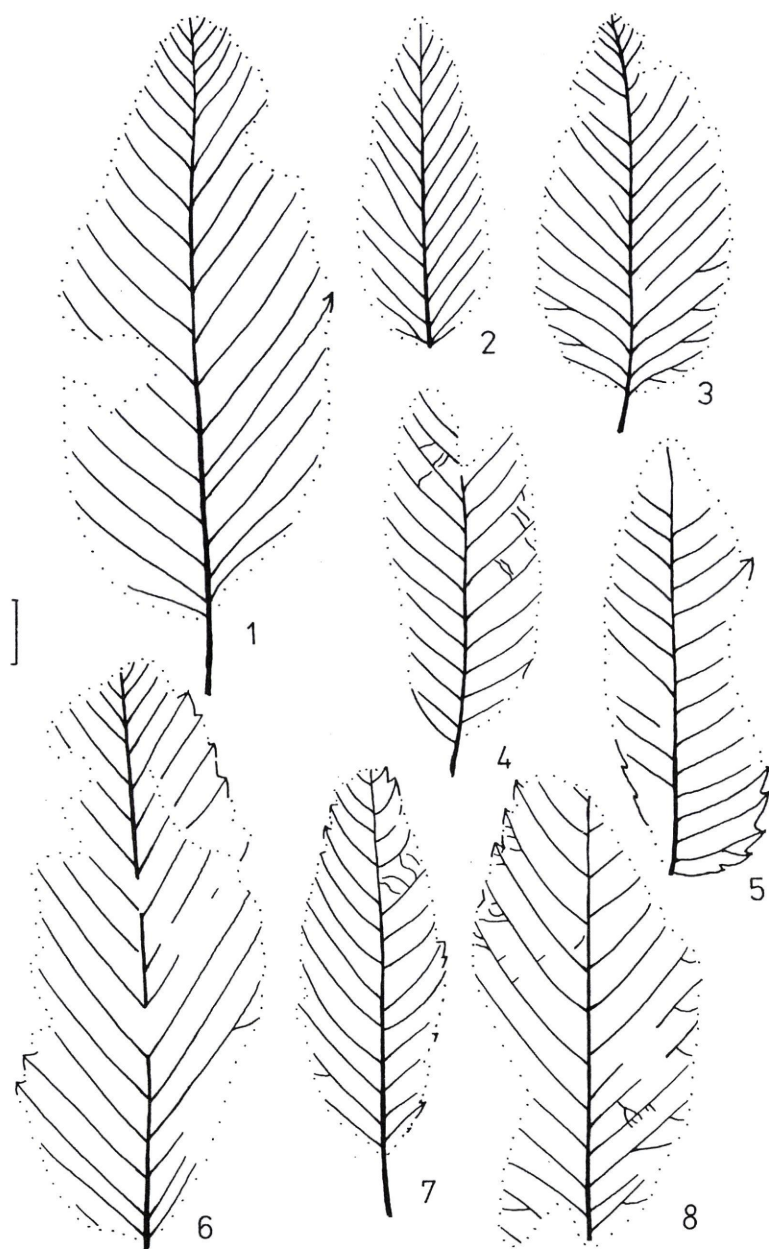


Fig. 10. *Ulmus pyramidalis* Goepp. (natural size). 1 = MM 61.788.2; 2 = MM 61.186.1; 3 = MM 61.194.1; 4 = MM 61.792.2; 5 = BP 2001.83.1; 6 = MM 61.787.1; 7 = BP 2001.26.1. – *Ulmus fischeri* Heer (natural size). 8 = BP 2001.7.1.

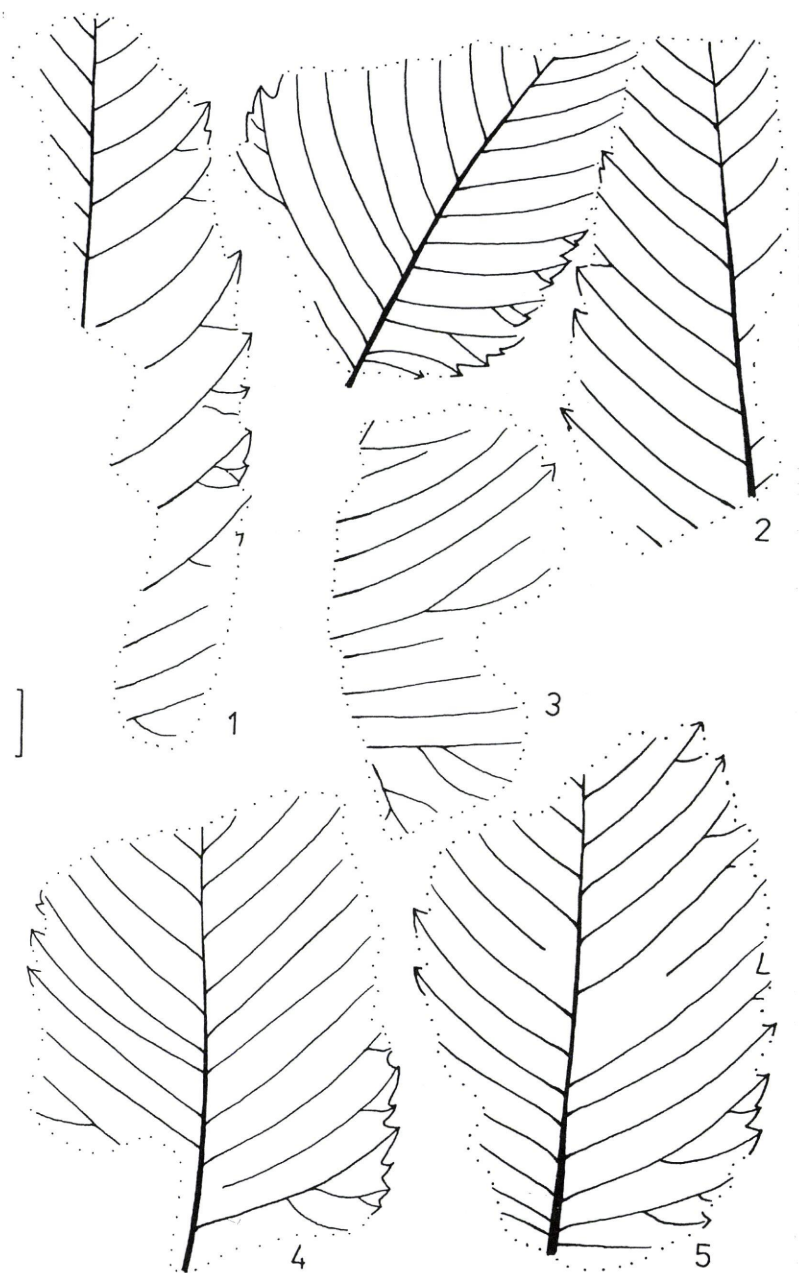


Fig. 11. *Ulmus fischeri* Heer (natural size). 1 = BP 2001.8.1; 2 = BP 2001.39.1; 4 = BP 2001.31.1; 5 = MM 56.696.1. – *Ulmus* sp. cf. *Ulmus fischeri* Heer (natural size). 3 = MM 2001.8.1.

Remarks. Determination of these specimens was not possible because they are too fragmentary with only a small part of the leaf visible on the impressions, most commonly without a margin. Most probably they belong to one of the above species.

TAPHONOMY

A study of the Egerian localities (HABLY 2001) has revealed differences in the composition of the sedimentary deposits. Some of them contain a high percent-

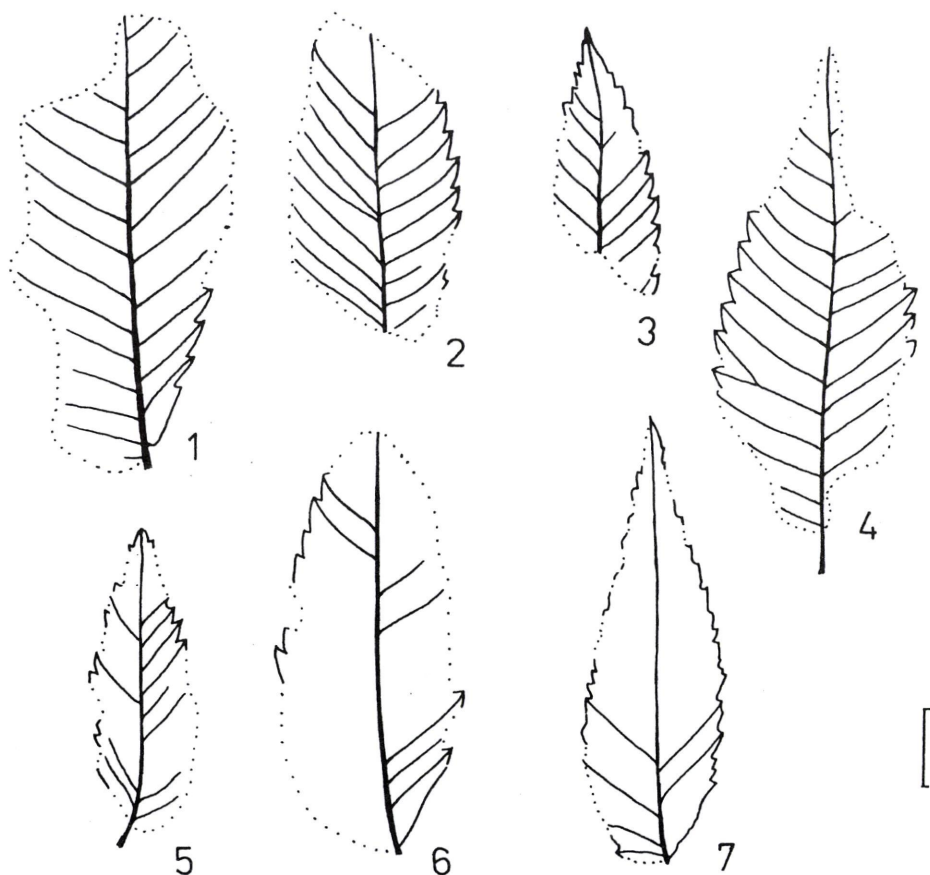


Fig. 12. *Ulmus* sp. (natural size). 1 = BP 2001.12.1; 2 = BP 2001.18.1; 3 = BP 2001.44.1; 4 = BP 2001.12.1; 5 = BP 2001.17.1; 6 = BP 2001.25.1; 7 = BP 2001.85.1.

age of mudstone (such as Pomáz with more than 70% mudstone), some a very low proportion (at Pusztaberki 19%), with intermediate values at the other sites. Leaf preservation varies in these localities. It is best where the proportion of mudstone is high with fewer and fewer taxa identifiable as it decreases. The genus *Daphnogene* is the only taxon which is identifiable even in the most coarse-grained, sandy sediments because its leaves were coriaceous. The genus *Ulmus* is another taxon which is still recognizable in these layers, but the leaf margin is mostly destroyed, so that recognition is often possible only from the general shape of the leaves, their primary and secondary venation. Complete leaves, having well visible leaf margins, with teeth, were collected at the Pomáz locality. Most of them (almost 200 specimens) belong to *Ulmus pyramidalis* Goepp., but 9 specimens determined as small-leaved elm, *U. cf. minuta* Goepp. (HABLY 1994) were also obtained. This second elm species was an accessory element in the flora of Pomáz.

The sedimentary conditions in the other fossil localities was not so favourable for fossil plant impressions. In the Eger-Wind brickyard the proportion of mudstone is only 52%, so the conditions for good preservation of leaf impressions are much poorer. From this locality ANDREÁNSZKY (1966) described several types of *Ulmus*. The present systematic revision confirms the occurrence of three species of elm in this flora: *Ulmus pseudopyramidalis* Z. Kvaček et Hably, *U. pyramidalis* Goepp., and *U. fischeri* Heer (KVAČEK and HABLY 1991). Plenty of leaves look complete, but their margin – the most important feature for the determination of *Ulmus* species – is not clearly visible. In most cases we can observe only some teeth, which are simple or possess an additional small tooth.

The leaves of all these species (*Ulmus pseudopyramidalis* Z. Kvaček et Hably, *U. fischeri* Heer and *U. pyramidalis* Goepp.) are easily separable in most of the specimens. The leaves of the first have mostly asymmetric bases, the secondary veins are distinctly arched and widely spaced and they have simple teeth, often with a small additional tooth. The leaves of *U. fischeri* have a very deeply cordate base and doubly serrate margin. Those of *U. pyramidalis* have mostly cuneate bases and straight and much more closely set secondary veins, particularly in the upper part of the leaf. They are similar to the leaves of *U. pyramidalis* Goepp. from the type locality in Sośnica in Poland (GOEPPERT 1855), in which doubly serrate leaf margins are clearly visible. The good state of preservation of the leaves in the Sośnica flora is associated with another type of sediment, a very fine clay. In this locality teeth are clearly visible, in many cases along the whole margin. The specimens from the Eger-Wind brickyard are poorly preserved in the coarse sediments so the leaf margin is not visible along the whole leaf length. The commonest species in this flora are *U. pseudopyramidalis* Z. Kvaček et Hably (81 specimens) and *U. pyramidalis* Goepp. (37 specimens).

A second important Egerian locality but with less well-preserved fossil leaves, Vértesszőlős, where the content of the mudstone is 20%. HABLY (1990) determined in this flora two fossil elm species: *Ulmus pyramidalis* Goepp. (60 specimens) and *U. plurinervia* Ung. (= *U. cf. minuta* Goepp., 6 specimens). The latter small-leaved elm is an accessory element in the flora. The leaf margins are not well-preserved, but the shape, base, and dense secondary venation of the leaves is so characteristic that we can assume that *U. pyramidalis* was present (e.g. HABLY 1990, p. 66, Figs 84, 87; p. 67, Figs 88, 90–93), while *Ulmus pseudopyramidalis* could also be present in this material. Some leaf impressions, described as cf. *Betula* (HABLY 1990, p. 63, Figs 95–96, 98; p. 69, Fig. 103), belong rather to *Ulmus*. They have no preserved margin, but features such as the arched secondaries with wide spacing between them suggest that they could belong to *U. pseudopyramidalis*.

Verőcsmaros is another fossil locality with very well-preserved plant material. The bearing sediment is mudstone. In this flora was found only one specimen of *U. fischeri* (HABLY 1982), with *U. pyramidalis* completely absent. Clearly, around this site of deposition of the fossil flora, *U. pyramidalis* did not exist.

Other Egerian floras at Andornaktálya, Nagysáp and Kesztlőc contain only one species of elm, namely *U. pyramidalis*. At these localities the proportion of mudstone in the sediment is 55–56%. From Andornaktálya were reported 32 specimens of *Ulmus pyramidalis* Goepp. (HABLY 1993a), from Kesztlőc 8 (HABLY 1988), but some other fragments, described as *Ulmus* sp., could also have been *U. pyramidalis* because of their dense, straight secondary venation. From Nagysáp only 2 specimens of *U. pyramidalis* have been mentioned (HABLY 1989).

There are also floras from Rétság and Pusztaberki, where the plant bearing sediment is very sandy. The content of the mudstone is only 31% at Rétság and 19% at Pusztaberki. Most of the leaf imprints at these localities are unidentified, except for some *Daphnogene* sp. and cf. *Ulmus* sp., comprising over 10% in both floras (HABLY 2001).

THE DISTRIBUTION OF FOSSIL *ULMUS* L. IN THE HUNGARIAN EGERIAN AND A PRESUMED PALAEOECOLOGICAL EXPLANATION

There is no doubt that the most abundant and widespread elm species, *Ulmus pyramidalis* Goepp., existed in Hungary during the Egerian. It occurs at six localities (Pomáz, Eger-Wind brickyard, Vértesszőlős, Andornaktálya, Kesztlőc, Nagysáp), and probably also at two others (Rétság, Pusztaberki). It is absent from only

one locality (Verőcsemaros) and is dominant in all sites except the Eger-Wind brickyard.

Ulmus pseudopyramidalis Z. Kvaček et Hably is dominant at the Eger-Wind brickyard, but *Ulmus pyramidalis* Goepp. is also common in both the middle and upper plant bearing layers. *U. pseudopyramidalis* was published only from here (KVAČEK and HABLY 1991), but we cannot exclude its presence at Vértesszőlős (see above). *Ulmus fischeri* Heer is an accessory element in the Hungarian Egerian (KVAČEK and HABLY 1991). *Ulmus* cf. *minuta* Goepp. (= *U. plurinervia* Ung.) is a rare accessory element, occurring at only two localities, Pomáz and Vértesszőlős.

Most of the above-mentioned palaeobotanical localities represent zonal vegetation of the Hungarian Egerian, but *Ulmus* is an element from edaphic intrazonal vegetation (HABLY 1993b), while *Ulmus pyramidalis* is a typical riparian element. Its co-occurrence with the remnants of highland vegetation, as in Pomáz, Kesztlőc, etc. is a consequence of the taphonomic conditions. They were all transported together to the place of fossilization.

Great quantities of the swamp element are present at the Eger-Wind brickyard. It is represented by the remains of *Blechnum*, *Asplenium*, *Pronephrium*, *Osmunda*, *Glyptostrobus*, *Alnus*, *Myrica*, *Acer tricuspidatum*, "*Rhamnus*" *warthae*, etc. *Ulmus pseudopyramidalis* occurs here in great quantity, much more abundantly, than the widespread *Ulmus pyramidalis*. Thus we may suppose that *Ulmus pseudopyramidalis* was also a swamp element and that this species could also be present at Vértesszőlős, because there swamp elements such as *Taxodium* and *Alnus* occur.

Table 1. Occurrence of *Ulmus* L. in the Hungarian Egerian floras.

Localities	<i>U. pyramidalis</i>	<i>U. pseudo-pyramidalis</i>	<i>U. fischeri</i>	<i>U. cf. minuta</i>
Pomáz	+++	—	—	+
Eger-Wind	++	+++	+	—
Vértesszőlős	++	+?	—	+
Kesztlőc	+	—	—	—
Andornaktálya	++	—	—	—
Nagysáp	+	—	—	—
Verőcsemaros	—	—	+	—
Rétság	+++	—	—	—
Pusztaberki	+++	—	—	—

Ulmus cf. *minuta* Goepp. (= *U. plurinervia* Ung.), an accessory element in the floras of Pomáz and Vértesszőlős, could be a riparian rather than a swamp element, because at both localities highland vegetation is more in evidence than swamp vegetation.

THE OCCURRENCE OF FOSSIL *ULMUS* L. IN OTHER TERTIARY LAYERS OF HUNGARY

The oldest appearance of *Ulmus* L. in Hungary can be dated to the Egerian age as leaves or fruits of elm have not been confirmed in earlier sediments. From the younger, Eggenburgian layers *Ulmus pyramidalis* Goepp. has been recorded from sandstone (Zagyvapálfalva Sandstone Formation) in the Ipolytarnóc locality (HABLY 1985b). This sandstone is the underlayer of the Gyulakeszi Riolittuff Formation, which bears a rich macroflora, but lacking *Ulmus* L.

In the younger Miocene floras several species of elm are known (HABLY 1985a), but only one of the above-mentioned. *Ulmus* cf. *minuta* Goepp. (= *U. plurinervia* Ung.), occurred in the younger Neogene. In the rich flora of Magyar-egregy, dated to the Middle Miocene, several elm fruits was collected by HABLY (unpubl.), but leaves are as yet unknown. Younger, Sarmatian floras usually contain small-leaved elms which have been determined as *Ulmus plurinervia*, *U. minuta*, or *U. braunii* (HABLY 1985a, ERDEI 1995). At most of the localities they are an accessory element.

The genus occurs in the Hungarian Tertiary in great quantity at Gércs and Pula where it is dated to the Pliocene (FISCHER and HABLY 1991, KVAČEK *et al.* 1994, HABLY and KVAČEK 1997). The elm, which is a dominant element in this flora, is a small-leaved form, namely *Ulmus braunii* Heer, which was also important in some Sarmatian floras, for instance at Erdőbénye (KOVÁTS 1856, ANDREÁNSZKY 1959, ERDEI 1995).

It seems that the species of elm which were dominant in the Egerian of Hungary did not survive into the younger Miocene floras. Their latest occurrence can be dated to the lower Miocene in this area.

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