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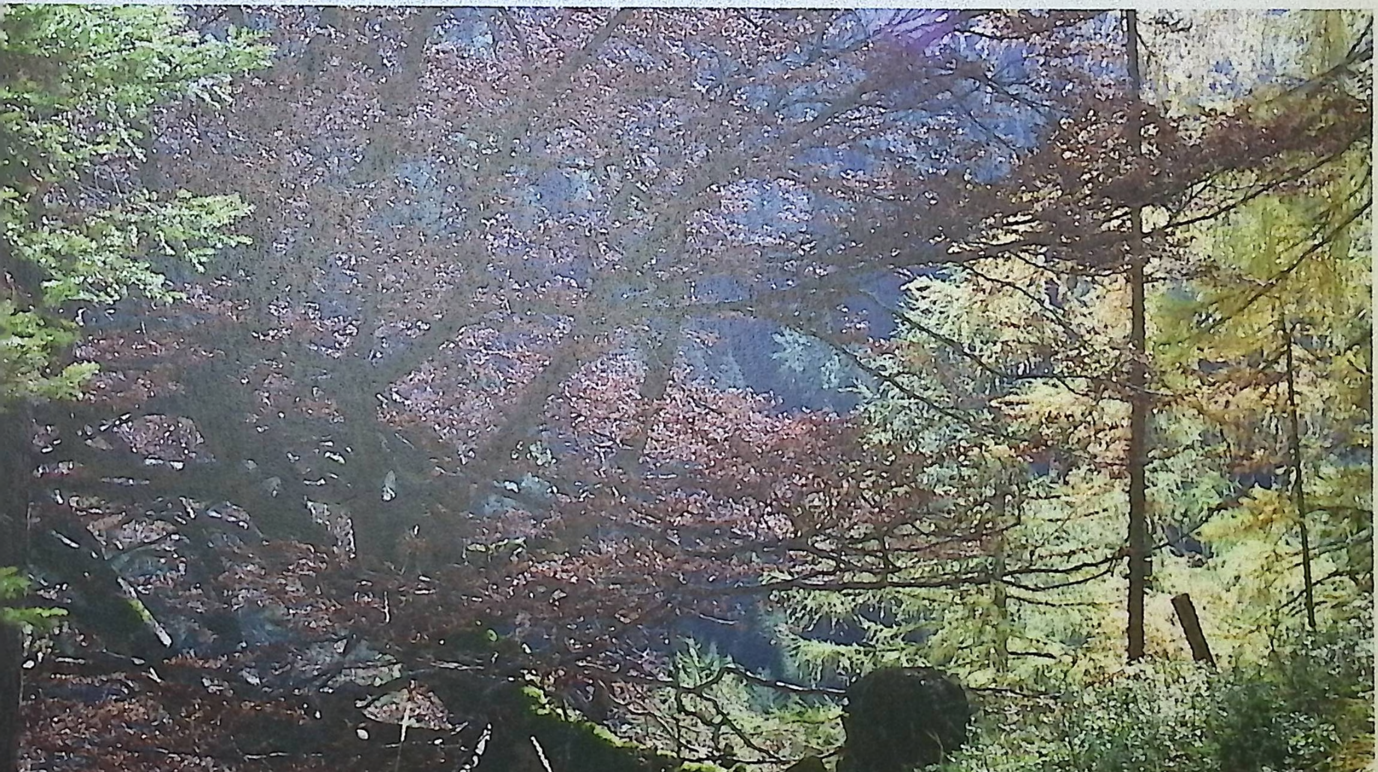

Thomas Denk

Revision of *Fagus* from the Cenozoic of Europe and southwestern Asia and its phylogenetic implications

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München 2004

Ich widme diese Arbeit über *Fagus*
dem am 11. April 2004
verstorbenen Kollegen

Erwin Knobloch †

Er hat die Basisarbeiten über *Fagus* in mehrfachen Publikationen vorgelegt.

Thomas Denk im Mai 2004

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Revision of *Fagus* from the Cenozoic of Europe and southwestern Asia and its phylogenetic implications

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Content

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Summary

A taxonomic revision of *Fagus* from the Cenozoic of Europe, southwestern Asia to Central Asia, using a molecular and morphologically based phylogenetic framework, shows a high level of redundancy of species names applied to Oligocene to Pliocene leaf and cupule/nut specimens. A clear demarcation between species can be observed at the boundary of Early Miocene to Middle Miocene. For the Oligocene to Early (Middle) Miocene a single species, *Fagus castaneifolia*, is recognized. This species ranges from Western Europe to eastern Kazakhstan and includes specimens previously referred to as *F. antipofii* p.p., *F. pristina,* and *F. saxonica*. This indicates that the dispersal of *Fagus* from the Northern Pacific region into Central Asia and Europe during the Oligocene was not linked to major radiations, and is in good agreement with molecular data. During the Neogene two polymorphic species, *F. gussonii* and *F. haidingeri* were present in Europe and southwestern Asia. These two species were geographically clearly distinct. *Fagus gussonii* displayed a southern distribution (Greece, Italy, Spain) that was linked to oceanic conditions, and had an isolated outpost on Iceland. Its occurrence is restricted to the Late Miocene. In contrast, *Fagus haidingeri* was widespread in Europe and western Asia from the Late Miocene to the Pliocene. In northern Italy and Greece *F. gussonii* had been replaced by *F. haidingeri* in the latest Miocene and the Pliocene. Previously recognized species such as *F. pliocenica, F. silesiaca, F. kraeuselii*, and others have to be included within *F. haidingeri*.

Fagus gussonii shows clear affinities to particular modern populations of the European-southwestern Asian *F. sylvatica* (Black Sea coastal areas) and to the modern Chinese *F. longipetiolata*. *Fagus haidingeri* resembles a number of modern European and East Asian species of the subgenus *Fagus* reflecting the late differentiation of modern species of the subgenus *Fagus*. The patterns of similarity between fossil taxa and modern species do not appear to be accidental, but correspond to patterns revealed by morphological and molecular phylogenetic studies.

Keywords: alpha taxonomy; evolutionary mode; Fagaceae; *Fagus castaneifolia*; *Fagus haidingeri*; *Fagus gussonii*; species concept; Cenozoic

1 Introduction

Understanding Cenozoic plant fossils is to a large extent based on the knowledge about modern members of a group of plants. *Fagus* (Fagaceae) is a small genus with around ten species in two subgenera. It occurs in western Eurasia, eastern North America and Mexico, and East Asia, and has an extensive fossil record from the Early Cenozoic onwards (SHEN, 1992; DENK & MELLER, 2001). Recently, morphological (SHEN, 1992; DENK, 1999a,b, 2003), molecular (STANFORD, 1998; MANOS & STANFORD, 2001; DENK et al., 2002; GRIMM, 2003), and paleobotanical/taphonomic studies (ZETTER, 1984; KVAČEK & WALTHER, 1991; WALTHER & ZASTAWNIAK, 1991; WALTHER & ZETTER, 1993; DENK & MELLER, 2001) have considerably changed our perspective on Cenozoic remains of *Fagus* represented by leaves, cupules/nuts, and pollen. Firstly, a phylogenetic framework is now available for *Fagus* (see appendix 1, 2). Morphological and molecular phylogenetic studies are consistent with two subgenera of *Fagus*, of which the subgenus *Engleriana* is confined to eastern Asia, whereas the subgenus *Fagus* is European-Asian-North American (Table 1). Species of the subgenus *Engleriana* are highly derived in many characters (e.g., stipitate buds, wax crystals and papillae on abaxial leaf epidermis, pseudocraspedodromous secondary venation, long colpi of pollen, long and slender cupule peduncle, reduced cupule appendages, reduced wings of the nuts), while they have retained a few primitive characteristics such as small stomata and small pollen. Fossils resembling members of the subgenus *Engleriana* have never been reported from Europe (cf. KVAČEK & WALTHER, 1991; DENK & MELLER, 2001). The members of the subgenus *Fagus*, except for the North American *Fagus grandifolia* Ehrh., display weak cladistic structure pointing to the late diversification of this group. This is reflected by a high amount of morphological and DNA sequence polymorphism (DENK, 2003; DENK et al., 2002; GRIMM, 2003). Secondly, taphonomic studies on leaves, cupules, and nuts of modern species reveal that several of the characters that can be used to distinguish modern species are lost during transportation and sedimentation of various plant organs (DENK & MELLER, 2001). "Diagnostic" features in fossils (cupules and nuts) previously used to distinguish species, therefore, may be taxonomically meaningless.

The main characteristics to distinguish fossil leaf morphotaxa of *Fagus* have been their size and shape, the number of secondary veins, the entire versus dentate leaf margin, the density of tertiary veins, and the size and type of stomata, among others. All these characters were sufficiently informative to define species as long as only little was known about the morphological variability of modern species. Also, early studies of fossil *Fagus* were restricted in the amount of modern species available for comparison to fossil species. For example, UNGER (1847), SAPORTA (1867), and HEER (1858, 1869, 1878a, b) were making a distinction mainly between fossils related to the European-western Eurasian *F. sylvatica* and the North American *F. grandifolia*. In addition to the limited number of modern species available for comparison (mainly of Chinese and Taiwanese species), difficulties arise because not enough is known about the intraspecific variability of modern species. This has been demonstrated for *Fagus* populations of western Eurasia (DENK, 1999a, b).

Here, I present a revised taxonomy of *Fagus* from the Cenozoic of Europe and western Eurasia (extending to Central Asia). Based on extensive fieldwork in China information on the variability of the modern Chinese species *F. longipetiolata, F. hayatae* subsp. *pashanica,* and *F. lucida* is provided for the first time, and affinities of fossil to modern species are evaluated. Fossil species from Europe to Central Asia are compared to fossils from the Cenozoic of East Asia and North America. Furthermore, I test whether the fossil record can be used to evaluate results from morphologically and molecular based phylogenetic studies using modern species only.

2 Material and Methods

Modern species of *Fagus* have been studied from herbarium material and collected in the field. For details on sample strategy, sample areas, and origin of herbarium material see DENK (2003) and DENK et al. (2002). Fossil material studied is housed in several museum and university collections or was collected in the field. For cupules and nuts see DENK & MELLER (2001), and DENK (2002). Leaf fossils studied are housed in the following institutions: Swedish Museum of Natural History, Stockholm (1); Museum für Mineralogie und Geologie, Dresden, Germany (2); Senckenberg Museum, Frankfurt, Germany (3); Institut und Museum für Geologie und Paläontologie der Universität Göttingen, Germany (4); Muséum national d'Histoire naturelle Paris, Laboratoire de Paléontologie, France (5); Dipartimento di Scienze della Terra, University of Torino, Italy (6); Geological Survey, Vienna, Austria (7); Institute of Paleontology, University of Vienna, Austria (8); Paleontological collection Landesmuseum Joanneum, Graz, Austria (9); Museum of Natural History, Ukrainian Academy of Sciences, Lviv, Ukraine (10); Komarov Botanical Institute, Russian Academy of Sciences, Saint-Petersburg, Russia (11); Vernadsky State Geological Museum, Moscow, Russia (12); Paleontological Institute and Museum, Russian Academy of Sciences, Moscow, Russia (13); University of Florida, Florida Museum of Natural History, Gainsville, USA (14). Further material from La Cerdaña, Spain; Vegora, Greece; Kymi, Greece; Makrilia, Crete, Greece; Malyi Shirak, Eastern Georgia; and Selárdalur, northwestern Iceland, has been collected in the field.

The origin and age of the material studied is shown in Fig. 1. A list of the specimens studied is provided in appendix 3. Symbols indicating "figured material" in Fig. 1 means that information on specimens is based on published figures and descriptions. For modern species the species concept of SHEN (1992) is followed (Table 1) except for the Chinese taxa *F. brevipetiolata, F. bijiensis,* and *F. tientaiensis*, all of which are considered to fall in *F. longipetiolata.* This is in accordance with HUANG et al. (1999) and DENK (2003).

Fagus remains from the Cenozoic of western Eurasia have traditionally been assigned to numerous different morphotaxa. In the present revision some species are recognized as being superfluous because they fall within the variability of other species. In such a case the International Code of Botanical Nomenclature (GREUTER et al., 2000) is followed. Mainly, the principle that the nomenclature of a taxonomic group is based upon priority of publication (Principle III) is followed. In addition, fossil taxa are treated as morphotaxa (Article 1.2.). Consequently, local populations of leaf morphotaxa that have recently been ascribed to new species based upon the presence of preserved epidermal structures cannot possibly replace previously described leaf morphotaxa based solely on gross morphology (see discussions to the species recognized in the present study).

3 Results

3.1 Morphological variability in modern species

Cupules and nuts, and pollen have been studied extensively in previous papers (DENK & MELLER, 2001; DENK, 2003), and epidermal features of modern *Fagus* have been described by ZETTER (1984), KVAČEK & WALTHER (1991), and DENK (2003), among others. While these character complexes are sufficiently informative to distinguish most of the modern species, they are either not preserved in the vast majority of fossils (leaf epidermal features) and in cases when they are preserved do not show significant changes from the Oligocene to the Pliocene (KVAČEK & WALTHER, 1991), or they have lost too many informative characteristics during transportation and fossilization as to be of any taxonomic value (cupule/nut complex, DENK & MELLER, 2001; DENK, 2002). Here, the focus lies on macroscopic leaf characters (Table 2).

Most leaf characteristics display high variability within species of *Fagus*. **(1)** Leaf size depends very much on the position of the leaves on the tree (see, for example, Fig. 8), and on microclimatic conditions (e.g., sun-exposed stand versus humid gorge, DENK, 1999a, b). Besides, species that typically form pure forests and attain largest tree hights, such as *F. grandifolia* and *F. sylvatica* exhibit the largest leaves, whereas the scattered populations of *F. hayatae* produce the smallest leaves. There is, however, a great overlap in leaf size range for most species (Table 2). **(2)** Also leaf shape can considerably vary within a species (Table 3). For example, *F. longipetiolata* may have trullate leaves with long petioles (Fig. 3, A, C). However, even within a single population trees show a variety of leaf types from trullate to elliptic (Fig. 3, E) and narrow elliptic ones (Fig. 3, F-I). Apart from these, narrow ovate leaves with attenuate apex and short petioles occur (Fig. 3, M). In *all* modern species broad-ovate (to oblong) leaves, mainly sun-leaves or leaves of fruiting twigs, co-occur with narrow-ovate (trullate), elliptic, or obovate (obtrullate) (shade) leaves, depending on the species, on the same tree. The presence or absence of certain (shade) leaf types is of diagnostic value to recognize certain groups of species (Table 3).

(3) A long and narrowly elongated leaf apex is found in *F. longipetiolata* (Fig. 3, M, N), *F. lucida* (Fig. 6, I), and *F. grandifolia* (Fig. 4, K), but absent in *F. sylvatica* and *F. crenata*. **(4)** The ratio length to width of lamina times 100 (leaf index; TANAI, 1974) is quite variable in *Fagus*, but mean and maximum values are clearly distinct between groups of species (see Table 2). While *F. longipetiolata* and *F. grandifolia* may have leaves with very high leaf index (Fig. 3, H, Fig. 4, K), *F. sylvatica* and *F. crenata* normally have much wider leaves (Figs. 8, 9). **(5)** Density of secondary venation differs insignificantly between species, while the maximum number of secondary veins is different among species, corresponding roughly to the maximum leaf sizes found in different species (Table 2). **(6)** The density of tertiary veins has been used by CHELEBAEVA (1980, 1982) to distinguish between fossil and modern species of *Fagus*. Although there is a consensus about the higher density of tertiary veins in the species of the subgenus *Engleriana* as compared to the subgenus *Fagus* (CHELEBAEVA, 1982; ZETTER, 1984; KVAČEK & WALTHER, 1991), the values given in these studies and own observations show a considerable discrepancy (see Table 2; Fig. 9, D, E). This may be due to different amounts of material examined but also due to different ways of counting tertiary veins. It is sometimes difficult to decide whether both of two branches of a tertiary vein actually are tertiary veins or only one of them. In this study, considerable differences in density of tertiary veins were encountered in sun and shade leaves of some species (*F. sylvatica, F. crenata*) or between geographical races (*F. grandifolia*).

(7) The type of secondary venation is brochidodromous and pseudocraspedodromous in the species of the subgenus *Engleriana*, and in *F. crenata* and *F. sylvatica*. In addition, in *F. sylvatica* dentate leaves with semicraspedodromous and craspedodromous secondary venation are found in eastern populations and in various ecotypes throughout its range (DENK, 1999a, b). The remaining species have semicraspedodromous and/or craspedodromous venation, but *F. longipetiolata* and *F. chienii* may as well have pseudocraspedodromous venation (see Fig. 3, B, D versus F-I). **(8)** The leaf margin between two adjacent secondary veins, the intersecondary margin region (IMR) is quite variable in most species, ranging from straight to convex to concave. In species of the subgenus *Engleriana* and *F. lucida, F. chienii, F. hayatae,* and *F. crenata* the IMR typically is convex (see Fig. 3, D; Fig. 5, E, L; Fig. 8). **(9)** The type and degree of dentation is extremely variable in *Fagus*. The species of the subgenus *Engleriana* and *F. crenata* are entire margined or crenulate, with the crenulate (apical) margin sometimes becoming (weakly) dentate (Fig. 8, A, B). *Fagus sylvatica* often has a crenulate leaf margin, but may also have dentate leaves (see Denk 1999a, b). For the remaining species four types of teeth are listed in Tables 2 and 3a. Type 1, "*longipetiolata*" type, refers to teeth that follow a convex IMR and have a blunt apex (Fig. 3, B, D). Type 2, "*lucida*" type refers to teeth following a convex IMR and having a sharp apex (typically in Fig. 6, K, L). At least some leaves of a tree of *F. lucida* (preferentially sun leaves) have narrow triangular teeth that are almost cuspidate (Fig. 6, H-L), or teeth that are "hooked" (Fig. 7, D, E). In type 3, "*hayatae*" type, the convex IMR often consists of a series of two or three arches that become shorter towards the following tooth, giving the margin a somewhat irregular appearance (Fig. 6, B, C) – a feature that is normally not found in *F. lucida* and *F. longipetiolata*, and makes these sympatric species easily to distinguish in the field. Teeth have a blunt apex (Fig. 5, B, E, H, N). Type 4, "*grandifolia*" type, refers to teeth having a straight to concave IMR and teeth with long basal side and short apical side, the apex of the tooth being sharp (Fig. 4, E). As mentioned before, leaf dentation is variable and the tooth types described here are "idealized" types that may overlap within species (Table 2). **(10)** The frequent occurrence of subsidiary teeth is typical of *F. lucida* and *F. hayatae*.

In addition, a few leaf epidermal features are listed in Table 2, illustrating the pronounced differences between the subgenera *Engleriana* and *Fagus*.

3.2 Systematic Paleobotany

The symbols correspond to those generally used in paleontology, contributing additional taxonomic information (RICHTER, 1948).

Explanations:

* = valid publication of the species
. = I am sure that this material belongs to the species
v = (vidi) material seen
? = it is doubtful if this material belongs to the species (sometimes also due to poor preservation)

3.2.1 *Fagus castaneifolia* UNGER 1847

(Figs. 10-11)

* *F. castaneifolia* UNGER, 1847, p. 104, pl. 28, fig. 1. Styria, Leoben, Austria – Karpatian. Landesmuseum Joanneum, Graz, Styria, Austria. **Holotype.**

. *F. antipofii* HEER, 1858, p. 572, pl. 8, fig. 2. Zharkuye, Turgaiskaya oblast, Kazakhstan – Chattian/Aquitanian.

.v *F. castaneifolia*? UNGER; SAPORTA, 1867, p. 70, pl. 5, fig. 7. Provence, Manosque, southern France – Aquitanian.

.v *F. pristina* SAPORTA, 1867, p. 69, pl. 6, figs. 1-3. Provence, Manosque, southern France – Aquitanian.

. *F. antipofii* HEER; KRYSHTOFOVICH, 1938, p. 95, pl. 2, figs. 2, 3. Ural Mts., Kinzebulatovo, European part of Russia – Chattian/Aquitanian.

.v "Gruppe *Fagus grandifolia* EHRH." p.p.; TRALAU, 1962, p. 159.

. *F. attenuata* subsp. *seussensis* KNOBLOCH, 1971, p. 8, pl. 1, fig. 11, pl. 3, figs. 1-3, 7, 8, 14, text fig. 1: 1. Bavaria, Seussen, Germany – Chattian-Burdigalian.

.v *F. antipofii* HEER; ZHILIN, 1974, p. 30, pl. 1, fig. 5, pl. 2, figs. 1, 2; text fig. 10, 1-3. Aral sea, Kumsuat bay, Aktyubinskaya oblast, Kazakhstan – Chattian .

.v *F. antipofii* HEER; ILJINSKAJA, 1982, p. 61, pl. 27, figs. 1-4, pl. 28, figs. 1, 2, text fig. 49: 1, 2. Ashutas, Vostochno-Kazakhstanskaya oblast, Kazakhstan – Chattian/Aquitanian.

.v *F. attenuata* GOEPPERT; ZETTER, 1984, p. 240, pl. 10, figs. 2-5, text fig. 9: 2-3. Salzburg, Lintsching, Austria – Karpatian.

.v *F. attenuata* GOEPPERT; ZETTER, 1984, p. 241, pl. 11, figs. 1-3, text fig. 9: 6. Styria, Fohnsdorf, Austria – Karpatian.

? *F. attenuata* GOEPPERT; ZETTER, 1984, p. 244, pl. 10, figs. 6, 7, text fig. 9: 5. Styria, Aflenz, Austria – Badenian.

.v *F. attenuata* GOEPPERT; ZETTER, 1984, p. 243, pl. 11, fig. 4, text fig. 9: 4. Styria, Leoben-Seegraben, Austria – Karpatian.

. *F. attenuata* GOEPPERT; KOVAR-EDER, 1982, p. 58, pl. 7, figs. 1-4, pl. 27, figs. 11-13. Upper Austria, Linz, Austria – Chattian (Egerian).

. *Quercus* vel *Castanea* sp. KOVAR-EDER, 1982, p. 64, pl. 7, figs. 10, 11, pl. 27, figs. 14, 15. Upper Austria, Linz, Austria – Chattian (Egerian).

. *F. attenuata* GOEPPERT; KVAČEK & WALTHER, 1989, p. 213, text fig. 1: a (cuticle preparation). Espenhain, Germany – Chattian.

.v *F. attenuata* GOEPPERT; KVAČEK & WALTHER, 1989, p. 213, text fig. 1: e. Saxonia, Bockwitz-Borna, Germany – Chattian.

.v *F. attenuata* GOEPPERT; KVAČEK & WALTHER, 1989, p. 213, text fig. 1: g. Saxonia, Borna-Ost, Germany – Chattian.

.v *F. saxonica* KVAČEK & WALTHER, 1991, p. 482, pl. 15, figs. 1-3, 5, 6, pl. 16, figs. 1-5 (cuticle preparations). Saxonia, Bockwitz-Borna, Germany – Chattian.

.v *F. saxonica* KVAČEK & WALTHER; MAI & WALTHER, 1991, p. 56, pl. 30, figs. 1-8, text fig. 3: 1-10 Saxonia, Bockwitz-Borna, Germany – Chattian.

.v *Castanea* vel *Quercus* sp., DJORDJEVIC-MILUTINOVIC et al., 2002, p. 135, Berane Basin, Montenegro – Early Miocene.

.v *Fagus*, ERDEI et al., 2002, p. 79, Kizilcahaman-Güvem area, western Anatolia, Turkey – Early Miocene.

.v *F. castaneifolia* UNGER; this study, Evia, Kymi, Greece – Aquitanian.

.v *F. castaneifolia* UNGER; this study, Rhodope Mts., Ognanovo (Gotse Delchev), Bulgaria – ?Aquitanian.

Excluded from *Fagus castaneifolia*:

?v *F. antipofii* HEER; HEER, 1869, p. 30, pl. 5, fig. 4a, pl. 7, figs. 4-8, pl. 8, fig. 1. Alaska, Englische Bucht (=Lower Kenai [Seldovian] Flora sensu WOLFE 1966) – Early to Middle Miocene.

?v *F. macrophylla* UNGER; HEER, 1869, p. 31, pl.8, fig. 2. Alaska, Englische Bucht (=Lower Kenai, Seldovian, Flora sensu WOLFE 1966) – Early to Middle Miocene.

?v *Fagus* sp; GRÍMSSON & DENK, submitted, Selárdalur, northwestern Iceland – 15 Ma.

Description - Leaves slender, narrow ovate to elliptic (to broad ovate); leaf index (length of lamina to width times 100) (180 to) 240 to 270 (to 300); leaf base obtuse, bluntly acute or slightly cuneate, very rarely slightly cordate; apex acute to acuminate to elongated acute; petiole up to 14 mm long, often not preserved; length of leaves up to 145 mm; number of pairs of secondary veins (12 to) 15 to 18 (to 21); number of tertiary veins per 1 cm 5 to 10, 5 to 8 in large (shade?) leaves, 7 to 10 in medium-sized leaves; secondary venation craspedodromous to semicraspedodromous; teeth normally sharp with straight basal side longer than apical side, narrow to broad triangular in shape, or rarely blunt to inconspicuous (dentate and entire margined specimens sometimes co-occurring in the same leaf assemblage); in some cases bluntness of the tooth apex is due to abrasion; subsidiary teeth normally absent; leaf margin between two adjacent teeth (intersecondary margin region) straight to concave, very rarely convex. Leaf epidermal features have been described by KVAČEK & WALTHER (1991, *F. saxonica*; Table 4).

Leaves associated with large (to 2.2 cm long) to small (1 cm) cupules belonging to *Fagus deucalionis* UNGER emend. DENK & MELLER (DENK & MELLER, 2001; DENK, 2002), and pollen of *Fagus bockwitzensis* WALTHER & ZETTER (1993). *Fagus bockwitzensis* is subspheroidal, 30 (to 35) µm in diamater with short colpi with acute ends; it is identical to pollen described by Schmid (2000) from the Late Rupelian of Germany (Cospuden, Saxonia).

Occurrence - Late Oligocene to late Early Miocene (Karpatian), Europe to Central Asia. (Pollen of *F. bockwitzensis* is known from the Late Rupelian of Germany.)

Affinities to modern and fossil species and phylogenetic context – The leaf morphotaxon *F. castaneifolia* does not show advanced features as found in the subgenus *Engleriana*, but resembles a number of species of the subgenus *Fagus*. Leaf shape and leaf dentation resemble most closely *F. longipetiolata* (Fig. 3, E, K, M) and *F. grandifolia* (Fig. 4, A-E, G-H); and, to a lesser degree, *F. lucida* (Fig. 7, F-H). The same can be observed for the leaf index (compare Tables 2, 3a). Cuticle features resemble those found in members of the subgenus *Fagus*, particularly *F. hayatae* and Mexican populations of *F. grandifolia* (KVAČEK & WALTHER,1991; WALTHER & ZETTER, 1993). Pollen co-occurring with leaves of *F. castaneifolia* is very similar to *F. hayatae* (compare WALTHER & ZETTER, 1993 for fossil and DENK, 2003 for modern pollen), and the cupule/nut complex to *F. crenata, F. grandifolia,* and *F. longipetiolata* (DENK & MELLER, 2001).

Identical leaf and cupule/nut types from Western Europe to eastern Kazakhstan during the Late Oligocene and Early Miocene indicate that the range expansion of *Fagus* to Central Asia and Europe in the course of the Oligocene was not linked to major radiations. In contrast, Eastern Asian, Alaskan, and Icelandic taxa from the Late Oligocene to the early Middle Miocene appear to belong to different lineages, leading perhaps to the modern subgenus *Engleriana* (*F. evenensis* CHELEBAEVA, 1980), or difficult to compare to any modern type of *Fagus* (*F. "antipofii"* from Alaska, HEER, 1869; WOLFE, 1966; *F. salnikovii* FOTJANOVA from Sakhalin, FOTJANOVA, 1988; *Fagus* sp. from Iceland, Selárdalur; see GRÍMSSON & DENK, submitted). The latter display enormously large leaves (more than 20 cm long), which may be a consequence of very humid and warm conditions at high latitudes.

Remarks - Specimens previously ascribed to different species are clearly linked by morphological transitions that do not exceed transitions observed within and between individuals of modern species. Diagnostic characteristics such as the leaf shape, the leaf index, the leaf margin and type of dentation, and the density of tertiary veins are consistent in specimens from southwestern Europe to Central Asia. Therefore, they are suggested to represent different morphotypes of one species. The material of the holotype of *F. castaneifolia* is part of the collections of the Landesmuseum Joanneum in Graz, Austria. It has been on loan to Reinhart Zetter, Institute of Paleontology at the University of Vienna, since the 1980s, when it was examined for a doctoral thesis. Since then it could not be located in Vienna. ZETTER (1984) mentioned that the figure in UNGER (1847) shows more of the details of the leaf margin than the actual specimen, which he figured as a photograph and a line drawing (ZETTER, 1984, text fig. 9: 1; pl. 10, fig. 1). Because of the incompletely preserved margin he was reluctant to assign *F. castaneifolia* to the genus *Fagus*. However, another leaf from the same locality (Leoben) is considered to belong to *F. attenuata* (text fig. 9, 4; pl. 11, fig. 4). Both the line drawing and photograph of the holotype of *F. castaneifolia* indicate that it most probably does belong to *Fagus*. The following characteristics are typical of *Fagus*: Firstly, the basalmost secondary veins are curved in such a way that they first bend towards the primary vein and then run straight towards the margin. The following secondaries are straight. This is a feature that can be found in other specimens of *Fagus*, for instance the two leaves from Lintsching figured in ZETTER (1984, text fig. 9: 2, 3; pl. 10, figs. 2-5) and in modern specimens. Secondly,

secondary veins are more densely spaced close to the apex. This is a typical feature of modern leaves with numerous (>14) pairs of secondary veins. Thirdly, the photograph of the holotype shows a characteristic dentation at the apical margin, where small, but sharp, eglandular teeth are followed by a straight intersecondary margin region. Straight intersecondary margin region can also be observed along the middle part of the margin. This is a typical feature of *Fagus* specimens from the Oligocene and Early Miocene of Europe, and of some modern species (see above). Moreover, the petiole of the holotype of *F. castaneifolia* is not particularly long as stated by UNGER (1847) for a rather large leaf with acute to cuneate base (see DENK, 1999a, b for relations between leaf base and length of petiole in modern *Fagus*). Finally, this leaf cannot belong to *Alnus* because of its regularly spaced secondaries and regular dentation.
Fagus castaneifolia typically exhibits long ovate slender leaf shapes (Fig. 10, A-G, Fig. 11, A). Often, these leaves co-occur with narrow elliptic forms (Fig. 10, H-M, Fig. 11, E), and sometimes with broad ovate/broad elliptic forms (Fig. 11, B-D, F, G). Similarly, the co-occurrence of narrow ovate to elliptic leaves with broad leaves is typical of modern species and can be found on the same tree, even the same twig. Moreover, the co-occurrence of markedly dentate leaves with almost entire-margined leaves is common rather than exceptional in several modern species (see Fig. 3, A, B versus F, H). This has also been reported for *F. sylvatica* (DENK, 1999a, b), *F. longipetiolata* (this study), *F. crenata* (SHEN, 1992), and occurs in populations of *F. grandifolia* from Mexico (pers. obs., herbarium FSU, Tallahassee).

Biogeographic framework - *Fagus* reached Europe from the east. It clearly appeared earlier in western North America (PIGG & WEHR, 2002, Middle Eocene; MEYER & MANCHESTER, 1997, Early Oligocene) and the Far East (FOTJANOVA, 1982; BUDANTSEV, 1997, Late Eocene; TANAI, 1995, Early Oligocene), and reached Europe only after the closure of the Turgai strait. First fossil evidence of *Fagus* in Europe is pollen from the Late Rupelian (Cospuden, Saxonia, SCHMID, 2000). Macrofossils appear for the first time in the Late Oligocene, both in Central Asia and Europe, and are morphologically homogeneous through the Early Miocene to early Middle Miocene (this study; see DENK & MELLER, 2001; DENK, 2002 for cupules and nuts). Mapping Oligocene and Early Miocene occurrences of *F. castaneifolia* on a paleogeographical map from the Aquitanian (Early Miocene) illustrates possible migration and dispersal pathways along the northern seashores of Paratethys and Mediterranean (Fig. 2).

3.2.2 *Fagus gussonii* MASSALONGO 1858 emend. KNOBLOCH & VELITZELOS 1986

(Fig. 12)

* *Fagus gussonii* MASSALONGO, 1858, p. 37; MASSALONGO & SCARABELLI, 1859, p. 202, pl. 25, figs. 2, 5, Senigallia, Italy - Messinian (Turolian).
. *F. gussonii* MASSALONGO emend. KNOBLOCH & VELITZELOS, 1986, p. 9, pl. 2, figs. 2-4, 6-8, pl. 5, fig. 11, pl. 6, fig. 5. Likudi, Greece – Late Miocene.

? *F. ambigua* MASSALONGO, 1853, p. 4, pl. 1, fig. 5. Senigallia, Italy - Messinian (Turolian).
. *F. ambigua* MASSALONGO, 1858, p. 38; MASSALONGO & SCARABELLI, 1859, p. 204, pl. 36, fig. 1. Senigallia, Italy - Messinian (Turolian).
. *F. betulaefolia* MASSALONGO, 1858, p. 38; MASSALONGO & SCARABELLI, 1859, p. 206, pl. 30, fig. 10. Senigallia, Italy - Messinian (Turolian).

. *F. chiericii* MASSALONGO, 1858, p. 39; MASSALONGO & SCARABELLI, 1859, p. 207, pl. 32, fig. 5. Senigallia, Italy - Messinian (Turolian).

. *F. deucalionis* auct. non UNGER; MASSALONGO, 1858, p. 37; MASSALONGO & SCARABELLI, 1859, p. 203, pl. 30, fig. 9. Senigallia, Italy - Messinian (Turolian).

. *F. incerta* MASSALONGO, 1858, p. 38; MASSALONGO & SCARABELLI, 1859, p. 205, pl. 30, fig. 3. Senigallia, Italy - Messinian (Turolian).

. *F. marsilii* MASSALONGO, 1858, p. 36; MASSALONGO & SCARABELLI, 1859, p. 201, pl. 9, fig. 19, pl. 21, fig. 18. Senigallia, Italy - Messinian (Turolian).

.v *Fagus* sp., FRIEDRICH, SÍMONARSON & HEIE, 1972, p. 8, pl. 1, fig. 3. Mókollsdalur, northwestern Iceland – 9-8 Ma.

? *F. attenuata* GOEPPERT; MÄDLER & STEFFENS, 1979, p. 15, pl. 4, fig. 2. Tavşanlı, Kütahya, northwestern Turkey – Late Miocene.

. *F. gussonii* MASSALONGO; BARRÓN & DIÉGUEZ, 1994, p. 23, text fig. 2: 1, 2, text fig. 3: 1-3, text fig. 4. La Cerdaña, Lérida, Northern Spain – Vallesian-Turolian.

. *F. pristina* SAPORTA; BARRÓN & DIÉGUEZ, 1994, p. 23, text fig. 2: 3, 4, text fig. 3: 4, 5, text fig. 5. La Cerdaña, Lérida, Northern Spain – Vallesian-Turolian.

.v *Fagus* sp., SACHSE & MOHR, 1996, p. 162, text fig. 3: 2, 5. Makrilia, southeastern Crete, Greece – Tortonian.

.v *F. gussonii* MASSALONGO; VELITZELOS & KVAČEK, 1999, p. 420, pl. 1, fig. 1. Vegora, north-western Greece – Late Miocene.

.v *F. gussonii* MASSALONGO; KVAČEK et al., 2002, p. 61, pl. 5, figs. 3-9, pl. 6, figs. 1-7, pl. 7, figs. 1-5, pl. 29, figs. 3-4 (cuticle preparations). Vegora, north-western Greece – Late Miocene

.v *F. gussonii* MASSALONGO; this study, Ellasona, Greece – Turolian.

.v *Fagus gussonii* MASSALONGO; GRÍMSSON & DENK, submitted. Mókollsdalur, Iceland – Late Tortonian (Turolian).

Non *Fagus*:

? *F. arduinorum* MASSALONGO, 1858, p. 37; MASSALONGO & SCARABELLI, 1859, p. 204, pl. 8, fig. 4. Senigallia, Italy - Messinian (Turolian).

Lectotype designated herewith: MASSALONGO & SCARABELLI, 1859, p. 202, pl. 25, fig. 2, Senigallia.

Description - Leaves broad ovate (rarely narrow ovate), broad elliptic, long elliptic, or obovate (shade leaves); leaf index (150 to) 200 (to 250); leaf base obtuse or acute (to elongated acute), in some specimens basal part of lamina becoming convex thereby creating a distinct oblong region which gives the leaf an inverted pear-shape; apex acute to acuminate; petiole 4 to > 10 mm long; leaves (30 to) 50 to 120 (140) mm long; number of pairs of secondary veins (6 to) 10 to 14 (to 16); number of tertiary veins per 1 cm (7 to) 9 to 12 (to 13) in medium-sized leaves; type of secondary venation pseudocraspedodromous to semicraspedodromous; teeth normally blunt or absent, rarely pointed triangular; teeth with convex basal side slightly longer than the apical side, intersecondary margin region straight to slightly convex; subsidiary teeth absent.

Cuticle features for *F. gussonii* have been reported by KVAČEK et al. (2002, see Table 4). Cupules associated with *F. gussonii* have only rarely been found (BARRÓN & DIÉGUEZ, 1994, Cerdaña; MAI & VELITZELOS, 1997, Vegora; this study). They are 1.8 to 2.2 cm long, which corresponds to the upper range of sizes reported for *F. deucalionis* UNGER emend. DENK & MELLER. No pollen associated with *F. gussonii* has been described.

Affinities to modern species and phylogenetic context - *Fagus gussonii* belongs to the subgenus *Fagus*. Leaf shape and leaf dentation closely resemble *F. longipetiolata* (Fig. 3, A, C, compare to Fig. 12, E-H) and *F. sylvatica* (Fig. 9, A-C, compare to Fig. 12, B, C, L, M; see also DENK, 1999a, b). The leaf index is similar to that encountered in *F. hayatae, F. crenata,* and *F. sylvatica*, and less so to *F. longipetiolata* among species of the subgenus *Fagus*. Cuticle features resemble those encountered in species of the subgenus *Fagus* except for *F. grandifolia* and *F. longipetiolata* (ZETTER, 1984; KVAČEK & WALTHER, 1991; KVAČEK et al., 2002). The cupule/nut complex is comparable to *F. sylvatica, F. longipetiolata* and *F. crenata* (DENK & MELLER, 2001). Affinities of *F. gussonii* to modern species plus its restricted geographical and stratigraphical range suggest this taxon reflects the diversification within the subgenus *Fagus* during the Late Miocene leading to modern species. The most characteristic similarity of *F. gussonii* is to modern populations of *F. sylvatica* from northern Turkey and the western Caucasus.

Occurrence - European endemic. Iceland, Mókollsdalur; Northern Spain, southern Italy, Greece, Crete, (?) to western Anatolia; Late Miocene.

Remarks - *Fagus gussonii* was validly published in 1858 by MASSALONGO and figured in MASSALONGO & SCARABELLI (1859). In the same paper five other species were published for the first time, all of which have been considered to belong to one species by later authors (e.g., MARTINETTO, 2003). Another (conspecific) species mentioned in MASSALONGO & SCARABELLI (1859) was *F. ambigua*. *Fagus ambigua* had already been validly published in 1853 in a paper by MASSALONGO (1853), in which MASSALONGO referred to an unnamed specimen figured in VIVIANI (1833). The latter was from Stradella (Pavia) and cannot with certainty be ascribed to *Fagus*. Here the name *F. gussonii* was chosen because it has recently been used by various authors also for areas outside Italy (KNOBLOCH & VELITZELOS, 1986; BARRÓN & DIÉGUEZ, 1994; KVAČEK et al., 2002), while the other names used by MASSALONGO (1858) have not been used later or restricted to Italian localities (e.g. *F. marsilii*, SORDELLI, 1898).

Fagus gussonii is geographically and stratigraphically most restricted among the three taxa of *Fagus* recognized for the Cenozoic of Europe. In the Late Miocene it appears to be a southern vicariant type of the central and eastern European populations of *F. haidingeri* and typically occurs at the margin of the geographical range of *Fagus*. *Fagus gussonii* is the only entity of *Fagus* in the Cenozoic of Europe that is straightly comparable to a few modern species. The two leaf-types recognized are clearly comparable to either *F. longipetiolata* from China to Vietnam or to *F. sylvatica* of the southern and eastern Black Sea coast.

3.2.3 *Fagus haidingeri* KOVÁTS 1856 sensu KNOBLOCH 1969

(Figs. 13-15)

* *F. haidingeri* KOVÁTS, 1856, p. 24, pl. 4, figs. 6, 7. Erdőbénye, Hungary – Sarmatian.

. *F. haidingeri* emend. KNOBLOCH, 1969, p. 79, pl. 36, figs. 2-8, 10, 11, pl. 37, figs. 1-11, pl. 38, figs. 2-11, text figs. 184 209. Moravská Nová Ves, Moravia, Czech Republic – Pannonian.

.v F. *pliocenica* SAPORTA, 1884, p. 18, pl. 6, figs. 1, 2, 4, 5, 3? (figures rather stylized). Cantal, Saint-Vicent, Pas-de-la-Mougudo, Niac, Central France – Pliocene.

? *F. antipofii* HEER; SORDELLI, 1893, p. 118, pl. 17, figs. 2-6, pl. 18, figs. 7-13. Di Montescano, Pavia, Italy – Messinian (Turolian).

? *F. marsiglii* MASSALONGO; SORDELLI, 1893, p. 120, pl. 18, fig. 14. Di Montescano, Pavia, Italy – Messinian (Turolian).

. *F. ferruginea* AIT. *miocenica* MENZEL, 1906, p. 48, pl. 3, figs. 4, 5, 10, 11, 12, pl. 8, fig. 15 (cupule). Senftenberg, Saxonia, Germany – Middle Miocene.

. *F. sylvatica* L. *fossilis* LAURENT & MARTY, 1923, p. 35, pl. 11, figs. 1-7. Reuver, southeastern Netherlands – Pliocene.

. *F. attenuata* GOEPPERT; WEYLAND, 1934, p. 53, pl. 5, figs. 1, 4, 5. Fischbach, Lower Rhine Embayment, Nordrhein-Westfalen, Germany – Middle Miocene.

. *F. orientalis* LIPSKY; STEFANOFF & JORDANOFF, 1935, p. 36, pl. 8, figs. 6, 7, pl. 9, figs. 2-5, text fig. 37. Plain of Sofia, Bulgaria – Pliocene.

.v *F. decurrens* REID & REID; MÄDLER, 1939, p. 84, pl. 7, figs. 28, 29. Frankfurt/Main, Germany – Pliocene.

.v *F. ferruginea* AIT. *fossilis* NATH.; MÄDLER, 1939, p. 83, pl. 7, figs. 21, 22. Frankfurt/Main, Germany – Pliocene.

? *F. attenuata* GOEPPERT; BERGER, 1957, p. 19, pl. 3, figs. 62-65. Gabbro, Tuscany – Messinian.

? *F. marsilii* MASSALONGO; BERGER, 1957, p. 20, pl. 3, fig. 66. Gabbro, Tuscany – Messinian.

. *F. angusta* ANDREÁNSZKY, 1959, p. 97, pl. 26, fig. 3, text fig. 83. Balaton-Dellö, Mikófalva, Sály, northeastern Hungary – Sarmatian.

. *F. aperta* ANDREÁNSZKY, 1959, p. 95, pl. 25, fig. 5, text fig. 79. Balaton-Dellö, Mikófalva, Sály, northeastern Hungary – Sarmatian.

. *F.* cfr. *grandifolia* EHRH.; ANDREÁNSZKY, 1959, p. 96, pl. 26, figs. 1, 2, text figs. 81, 82. Balaton-Dellö, Mikófalva, Sály, northeastern Hungary – Sarmatian.

. *F. latissima* ANDREÁNSZKY, 1959, p. 96, pl. 25, fig. 7, text fig. 80. Balaton-Dellö, Mikófalva, Sály, northeastern Hungary – Sarmatian.

. *F. oblonga* ANDREÁNSZKY, 1959, p. 95, pl. 25, fig. 6. Balaton-Dellö, Mikófalva, Sály, northeastern Hungary – Sarmatian.

. *F. palaeojaponica* ANDREÁNSZKY, 1959, p. 96, pl. 25, fig. 4. Balaton-Dellö, Mikófalva, Sály, northeastern Hungary – Sarmatian.

. *F. decurrens* REID & REID; SZAFER, 1961, p. 40, pl. 11, fig. 14. Stare Gliwice, Upper Silesia, Poland – Miocene.

. *F.* cf. *ferruginea* AIT.; SZAFER, 1961, p. 40, pl. 11, figs. 10, 11. Stare Gliwice, Upper Silesia, Poland – Miocene.

.v "Gruppe *F. sylvatica* L." p.p., TRALAU, 1962, p. 148, pl. 1, fig. A, pl. 2, figs. A-H, pl. 3, figs. A-E. Willershausen, Germany – Pliocene.

.v "Gruppe *F. grandifolia* EHRH."p.p., TRALAU, 1962, p. 159, pl. 4, figs. A-C. Willershausen, Germany – Pliocene.

.v *F. herthae* ILJINSKAJA, 1964, p. 132, pl.3, figs. 2-4, pl. 6, figs. 6, 7. Swoszowice/Cracow, Poland – Badenian.

. *F. orientalis* LIPSKY *fossilis* PALIBIN; KOLAKOVSKI, 1964, p. 82, pl. 26, figs. 5, 6 (poorly preserved leaf fragments). Kodor, northwestern Georgia (Abkhazia) – Meotian (Pannonian).

.v *F. orientalis* LIPSKY *fossilis* PALIBIN; KUTUZKINA, 1964, p. 192, pl. 5, figs. 2, 5, 10, 13, 15. Armavir, Northern Caucasus – Sarmatian.

.v *F. orientalis* Lipsky var. *fossilis* Baikovskaya; Kryshtofovich & Baikovskaya, 1965, p. 49, pl. 10, figs. 10, 11, pl. 11, figs. 1-3, pl. 12, figs. 1-8, pl. 13, fig. 1. Krynka, Northern Caucasus – Early Sarmatian.

.v *F. orientalis* Lipsky *fossilis* Palibin; Kolakovski & Ratiani, 1967, p. 39, pl. 4, fig. 1. (plus extremely small cupules, pers. obs. T. Denk, 2001). Malyi Shirak, southeastern Georgia – Akchagylian.

. *F. attenuata* Goeppert; Givulescu & Ghiurca, 1969, p. 33, pl. 7, figs. 9-12, pl. 8, figs. 4, 6, 7, pl. 9, figs. 1, 2, pl. 12, fig. 9. Chiuzbaia, northwestern Romania – Pliocene.

. *Fagus* sp., Givulescu & Ghiurca, 1969, p. 34, pl. 9, figs. 3-6. Chiuzbaia, northwestern Romania – Pliocene.

. *F. haidingeri* emend. Knobloch; Zastawniak, 1972, p. 23, pl. 4, figs. 3-7, pl. 5, figs. 1-6, pl. 17, figs. 5, 6, pl. 18, figs. 1-5. Domański Wierch, western Carpathians, Poland – Pliocene.

.v *F. attenuata* Goeppert; Iljinskaja, 1982, p. 66, pl. 25, figs. 1-5, 7-9, not 6. Sosnica close to Wroclav, Poland – Late Miocene; pl. 26, figs. 1-3. Kodor, northwestern Georgia (Abkhazia) – Meotian (Pannonian); text fig. 53: 1-11. Kortumova Hora, Hlyns'ke, western Ukraine – Early Badenian.

.v *F. orientalis* Lipsky var. *palibinii* Iljinskaja, 1982, p. 62, pl. 24, figs. 3-6. Kermal-Naftalan, Azerbaidzhan – Akchagylian.

. *F. attenuata* Goeppert; Hummel, 1983, p. 22, pl. 8, figs. 1-7, pl. 9, figs. 1-5, pl. 10, figs. 1-6, pl. 11, figs. 1-5, pl. 12, figs. 1-4 (cuticle preparations), text fig. 9: 1-25. Ruszów, Lower Silesia, southwestern Poland – Pliocene.

.v *F. attenuata* Goeppert; Shwareva, 1983, p. 82, pl. 8, figs. 1-9, pl. 9, figs. 1-10, pl. pl. 17, fig. 6, pl. 24, figs. 4-6, pl. 25, fig. 11, pl. 27, figs. 3-5, pl. 44, fig. 3, pl. 47, figs. 2, 3, pl. 77, figs. 5, 6, text figs. 15: 1-9, 16: 1-13. Kleparivs'ka Vysochyna, close to Lviv, western Ukraine – Early Sarmatian; Kortumova Hora, Hlyns'ke, close to Lviv, western Ukraine – Early Badenian; Roshnyato close to Ivano-Frankivs'k, western Ukraine – Late Badenian; Kosiv and Mychyn, south of Kolomyia, western Ukraine – Late Badenian; Velyka Uholka east of Khust, western Ukraine – Late Badenian.

.v *F. haidingeri* emend. Knobloch; Zetter, 1984, p. 245, pl. 11, figs. 5-8, pl. 12, figs. 1-12, pl. 13, figs. 1-11, text fig. 10: 1-14, text fig. 11: 1-9, text fig. 12: 1-4, text fig. 13: 1-15, text fig. 14: 1/11, text fig. 15: 1-4. Vienna, Lower Austria, Upper Austria, Burgenland; Austria – Pannon.

.v *F. attenuata* Goeppert; Knobloch, 1988, p. 10, pl. 1, fig. 4, pl. 3, fig. 4, pl. 9, figs. 4, 5, 10, pl. 13, fig. 4. Aubenham, Lower Bavaria, Germany – Pannonnian-Pontian.

. *F. haidingeri* emend. Knobloch; Kovar-Eder, 1988, p. 31, pl. 2, figs. 11-17, pl. 4, figs. 3, 4. Schneegattern, Lohnsburg, Grossenreith, Upper Austria – Pannonian.

.v *F. attenuata* Goeppert; Mai & Walther, 1988, p. 119, pl. 21, figs. 1-13, text. figs. 38-40. Berga, Thuringia, Germany – Upper Pliocene.

.v *F. kraeuselii* Kvaček & Walther, 1991, p. 488, pl. 19, figs. 1-5, pl. 20, figs. 1, 2 (cuticle preparations). Niederrad, Frankfurt/Main, Germany – Pliocene.

. *F. menzelii* Kvaček & Walther, 1991, p. 485, pl. 17, figs. 1-6, pl. 18, figs. 1-5 (cuticle preparations). Kausche/Welzow, Brandenburg; Zschipkau/Senftenberg, Saxonia; Fischbach, Lower Rhine Embayment, Nordrhein-Westfalen, Germany. ? Hrádek, Czech Republic – Middle to Late Miocene.

.v *F. silesiaca* Walther & Zastawniak, 1991, p. 156, pl. 1, figs. 1-3, 4-6 (cuticle preparations), pl. 2, fig. 1, text fig. 1. Sośnica, Poland – Late Miocene.

.v *F. silesiaca* var. *gozdnicensis* Łańcucka-Środoniowa et al., Łańcucka-Środoniowa et al., 1992, p. 26, pl. 8, fig. 6, pl. 9, fig. 3, 4, pl. 11, fig. 2-4, pl. 12, fig. 1-4, text fig. 7. Gozdnica, Lower Silesia, Poland – Late Miocene.

.v *F. pliocenica* subsp. *multinervis* Knobloch, 1998, p. 27, pl. 9, fig. 5, pl. 10, fig. 3. Willershausen, Germany – Pliocene.

.v *F. pliocenica* subsp. *willershausensis* Knobloch, 1998, p. 24, pl. 5, fig. 2, pl. 9, figs. 1-4, pl. 10, figs. 1, 4, 6, 8, pl. 13, fig. 5, pl. 15, fig. 7, pl. 16, fig. 4. Willershausen, Germany – Pliocene.

. *F. menzelii* Kvaček & Walther; Van der Burgh, 2001, p. 289, pl. 2, figs. 1, 2, 7. Hambach, Lower Rhine embayment, Germany – Late Miocene.

. *F. kraeuselii* Kvaček & Walther; Van der Burgh, 2001, p. 289, pl. 2, figs. 3-6, 8, 9. Brunnsum, south/eastern Netherlands; Eschweiler, Hambach, Germany – Late Miocene to Early Pliocene.

. *F.* cf. *attenuata* Goeppert; Fischer & Butzmann, 2000, p. 44, pl. 10, figs. 10-13, text. figs. 56-58. Meleto, Italy – Late Neogene.

. *F.* cf. *haidingeri* Kováts sensu Knobloch; Fischer & Butzmann, 2000, p. 44, pl. 11, figs. 1-4, text. figs. 59-62. Meleto, Italy – Late Neogene.

. *F. antipofii* Heer; Brambilla & Gallo, 2002, p. 221, pl. 9, figs. 1-3, text fig. 13a. Nizza Monferrato, Asti, Piedmont, Italy – Messinian.

. *Fagus haidingeri* Kováts; Brambilla & Gallo, 2002, p. 222, pl. 9, fig. 4. Nizza Monferrato, Asti, Piedmont, Italy – Messinian.

. *F. latissima* Andreánszky; Brambilla & Gallo, 2002, p. 222, pl. 10, fig. 3. Nizza Monferrato, Asti, Piedmont, Italy – Messinian.

. *Quercus* cf. *pseudocastanea* Goeppert; Brambilla & Gallo, 2002, p. 224, pl. 10, fig. 4, text fig. 14a. Nizza Monferrato, Asti, Piedmont, Italy – Messinian.

.v *F. pliocenica* Saporta; Martinetto, 2003, pl. 4, figs. 3-6. Asti, Piedmont, Italy – Pliocene.

?v *F. haidingeri* Kováts; this study. Castagnito and Scaparoni d'Alba, Piedmont, Italy – Messinian.

.v *F. haidingeri* Kováts; this study. Valmanera, Asti, Piedmont, Italy – Pliocene (coll. Cecilia Binello, Edoardo Martinetto, stored at Dipartimento di Scienze della Terre, University of Torino).

.v *F. haidingeri* Kováts; this study, Neu-Isenburg, south of Frankfurt/Main, Germany – Pliocene.

.v *F. haidingeri* Kováts; Denk & Velitzelos, in progress, Atalanti, Greece – Pliocene.

Uncertain affinities:

? *F. juliae* Yakubovskaya, 1975, p. 529, pl. 10, figs. 1-7, text fig. 3: a-g, text fig. 4: a-h. Kamennyi Brod, Tambov oblast, Russia – Middle Miocene.

Lectotype designated herewith: Kováts, 1856, p. 24, pl. 4, fig. 6, Erdöbénye.

Description - Leaves narrow to broad ovate to broad elliptic (to narrow elliptic); leaf index (155 to) 210 (to 270); leaf base acute, obtuse, cuneate or cordate; apex acute to acuminate; petiole short (around 4 mm) to long (to 15 mm); leaves often medium-sized (50 to 80 mm), less frequently large leaves (up to 125 mm); number of pairs of secondary veins (6 to) 8 to 12 (to 16); number of tertiary veins per 1 cm 9 to 12 (to15) in medium-sized leaves; type of secondary venation semicraspedodromous to pseudocraspedodromous, less frequently craspedodromous; teeth normally blunt (rarely sharp), very similar to those of the modern *F. hayatae* subsp. *pashanica, F. longipetiolata* and *F. chienii*, or absent and then margin similar to *F. crenata* and *F. sylvatica*; teeth with relatively short basal side and short apical side, the basal side of the tooth follows a slightly to pronounced convex intersecondary margin region; the convex intersecondary margin region also being present in entire margined leaves. Subsidiary teeth rather common in dentate leaves. Leaf epidermal features have been described by HUMMEL (1983), KVAČEK & WALTHER (1991), WALTHER & ZASTAWNIAK (1991), and ŁAŃCUCKA-ŚRODONIOWA et al. (1992) (Table 4). Associated with small (< 1 cm) to large (to 1.8 cm) cupules belonging to *F. deucalionis* UNG. emend. DENK & MELLER (2001). ŁAŃCUCKA-ŚRODONIOWA et al. (1992) reported pollen associated with leaves of *F. haidingeri*, which is subspheroidal, 34 to 40 µm in polar diameter, and 32 to 37 µm in equatorial diameter, with rather short colpi as in species of the subgenus *Fagus* (DENK, 2003). Values in GORTEMAKER (1986) for Late Miocene to Pliocene pollen are slightly smaller.

Affinities to modern species and phylogenetic context - *Fagus haidingeri* belongs to the subgenus *Fagus*. Leaf shape and leaf dentation resemble *F. hayatae* subsp. *pashanica* (Fig. 5, A-S, Fig. 6, A-G), *F. longipetiolata* (Fig. 3, A, C, N, O), *F. chienii* (Fig. 6, N-P, Fig. 7, M-P), *F. crenata* (Fig. 8, A-I), and *F. sylvatica* (western populations, see DENK, 1999b). The leaf index corresponds to that found in modern *F. hayatae* (Tables 2, 3a). Cuticle features resemble those encountered in species of the subgenus *Fagus* except for *F. grandifolia* and *F. longipetiolata* (KVAČEK & WALTHER, 1991; ZETTER, 1984). The cupule/nut complex is very similar to *F. hayatae* and *F. crenata* (DENK & MELLER, 2001) and pollen is most similar to *F. hayatae, F. crenata,* and *F. longipetiolata* (DENK, 2003). Affinities of *F. haidingeri* to modern species point to a close relationship of this fossil species to modern Eurasian members of the subgenus *Fagus*, but not to the North American *F. grandifolia*. This is in good agreement with molecular data that suggest a very late differentiation among modern Eurasian species of the subgenus *Fagus*.

Occurrence - Middle Miocene to Late Pliocene, Europe to eastern Caucasia.

Remarks - This taxon comprises the bulk of specimens previously assigned to *F. attenuata*. The type specimen of *F. attenuata* figured in GOEPPERT (1855) was later found to belong to *Alnus* (WALTHER & ZASTAWNIAK, 1991). *Fagus haidingeri* has been validly published by KOVÁTS in 1856. Although the type specimens are lost from the collection of the museum in Budapest (pers. com. L. HABLY 2002), there is no doubt that the two leaves figured by KOVÁTS belong to *Fagus*. Specimens from different areas that have previously been assigned to different morphospecies show patterns of intraspecific variability as encountered in modern species (cf. DENK, 1999a, b). Specifically, a number of characteristics or a combination of characteristics are sufficiently stable to define *F. haidingeri* as a good species (see Tables 3, 3a). These are, among others, the typical tooth shape in connection with a convex intersecondary margin region, and the occurrence of "*F. hayatae*-like" and "*F. crenata*-like" leaf shapes in all assemblages containing this species.
Fossils belonging to *F. haidingeri* traditionally were compared to the modern species *F. grandifolia* (syn. *F. ferruginea* AITON), and to *F. sylvatica* and *F. orientalis*, which is reflected in applying these names to fossil species (see list of synonyms). Researchers such as ANDREÁNSZKY (1959) recognized up to nine different species for rather limited geographic areas. A possible explanation for this may be that *F.*

haidingeri shows similarities to a number of modern species of the subgenus *Fagus*. Among these, conspicuous similarities are with *F. hayatae* subsp. *pashanica*. This applies to leaf shape and size, the number of pairs of secondary veins, the tooth type, and the intersecondary margin region (compare Fig. 5, A-S, Fig. 6, A-G to Fig. 13, F-I, Fig. 14, D, M), and has been recognized earlier by ŁAŃCUCKA-ŚRODONIOWA et al. (1992) for specimens from Poland. In addition, similarities to *F. chienii* (compare Fig. 6, N-P, Fig. 7, M-P to Fig. 13, I-M, Fig. 14, A-C, F-H) are observable, i.e. the leaf dimorphism found in the isotype of *F. chienii* is very similar to that found in various fossil leaf assemblages (for instance Willershausen, Krynka). Larger specimens of *F. haidingeri* such as those described by ZETTER (1984) resemble long ovate-trullate morphotypes of *F. longipetiolata, F. hayatae* subsp. *pashanica*, and *F. lucida* based on leaf shape, leaf dentation, and IMR (Fig. 14, I-L). From different areas and time periods (e.g. Willershausen, Krynka, Cantal) leaves exhibiting a mosaic of morphological features found in the modern *F. crenata, F. longipetiolata,* and *F. sylvatica* are known (e.g., typical "*crenata*-like" leaf types in Fig. 13, A-D). Leaves from Frankfurt are very similar to the modern *F. crenata* (Fig. 13, B) and to *F. hayatae* (Fig. 14, D, E). These leaf types are clinally connected (e.g. Fig. 13, G).

In Greece and Italy (Fig. 15) both *F. haidingeri* and *F. gussonii* occur. This is of particular interest, because *F. gussonii* is restricted to the Late Miocene, and appears to be "replaced" by *F. haidingeri* in the Pliocene of Greece (Atalanti, DENK & VELITZELOS, in progress). The same may be true for Italy, where *F. gussonii* is found in the Late Miocene of Senigallia (MASSALONGO & SCARABELLI, 1859). However, for a number of Late Miocene to Pliocene Italian localities the picture becomes more complicated. Specimens from the Pliocene of Northern and Central Italy that have recently been ascribed to various species (FISCHER & BUTZMANN, 2000; MARTINETTO, 2003) clearly belong to *F. haidingeri* (Table 5). SORDELLI (1896) described *Fagus* from the Messinian of Montescano. The specimens figured by SORDELLI cannot be ascribed with certainty to *F. gussonii* nor to *F. haidingeri*. They display a leaf index that is much higher than in *F. gussonii* and *F. haidingeri*; leaf shape is more similar to *F. haidingeri* whereas the number of secondaries corresponds to *F. gussonii*. BRAMBILLA & GALLO (2002) describe *Fagus* from Nizza Monferrato. The few specimens figured by them are narrow ovate, narrow elliptic, and wide elliptic. While the narrow ovate leaf with numerous secondary veins (*F. antipofii*) resembles some leaves of *F. haidingeri*, the leaf ascribed to *F. latissima* cannot be assigned to either *F. gussonii* or *F. haidingeri*. Finally, the specimens from Castagnito and Scaparoni d'Alba, Messinian (Fig. 15, A-L) may belong to either *F. gussonii* or *F. haidingeri*, and look very similar to the specimens figured in SORDELLI (1896).

It appears that *F. gussonii* was restricted to the Late Miocene and centred towards the more southern parts of Italy, while hybrid zones formed between *F. haidingeri* and *F. gussonii* in the Late Miocene of Italy. More detailed research including the rich collections of cupules and nuts housed at the Dipartimento di Scienze della Terra, University of Torino, is needed to solve this problem.

Specimens described as *F. juliae* by JAKUBOVSKAYA (1975) are difficult to place within either *F. castaneifolia* or *F. haidingeri*. The material (around 350 specimens) on which this species was based has been lost or destroyed after Jakubovskaya's death. A small part of badly preserved specimens is kept in a private collection in Moscow, while all the specimens originally stored at the Earth Museum of the Moscow University are lost (pers. com. Aleksej Hvalj). These specimens were leaf impressions in coarse sandstone, with no details of higher order venation and tooth architecture preserved. Leaves are large (to 18 cm long), elliptic, with a dentate margin. The leaf index is (175 to) 200 to 250 (to 300), which is larger than normally found in *F. haidingeri*.

4 Discussion

4.1 Species concepts

A number of accounts on taxonomic relationships between modern and fossil *Fagus* focussed on single characters as criterion for species delimitation (e.g., the ratio of the length to the width of a leaf = leaf index; TANAI, 1974), without having sufficient information on the variability of these morphological characters in modern *Fagus*, or considering evidence from other character complexes. As a consequence, a very narrow species concept was applied, treating, for example, specimens that display slightly different leaf shapes as different species/subspecies. Examples are the works of MASSALONGO (1858), MASSALONGO & SCARABELLI (1859), and ANDREÁNSZKY (1959), and, among most recent papers KNOBLOCH (1998) and BRAMBILLA & GALLO (2002). The same applies to several studies on phylogenetic relationships in *Fagus*. For example, KOLAKOVSKI (1960) recognized two major clades within fossil and modern *Fagus* defined by having brochidodromous versus craspedodromous secondary venation. However, some of the species falling in the "group of craspedodromous venation" are not necessarily so (*F. longipetiolata*), and the "brochidodromous" lineage of KOLAKOVSKI includes two species of the subgenus *Engleriana* that are not at all related to the remaining brochidodromous species *F. sylvatica* (*F. orientalis, F. moesiaca*) and *F. crenata* (subgenus *Fagus*), differing not only genetically but also by leaf epidermal features and the cupule/nut complex (KVAČEK & WALTHER, 1991; DENK & MELLER, 2001; DENK, 2003). TRALAU (1962) also recognized two main groups within *Fagus* from the Cenozoic of Europe, referred to as "Gruppe *F. sylvatica*", and "Gruppe *F. grandifolia*". This was based on differences between the length/width ratios of leaves. According to TRALAU (1962) specimens ascribed to the "Gruppe *F. sylvatica*" display close affinity to the modern *F. sylvatica* and to "species closely related to *F. sylvatica*", which he considered to be *F. crenata* and *F. longipetiolata* (subgenus *Fagus*), but also *F. japonica* and *F. engleriana* (subgenus *Engleriana*). Fossils from the Oligocene to the Pliocene were ascribed to a second group "*Fagus grandifolia*" by TRALAU (1962), and compared to the modern *F. grandifolia*. Among the specimens included here were those from Frankfurt ascribed by MÄDLER (1939) to *F. ferruginea fossilis*, a few specimens from Willershausen, and *F. pliocenica* (SAPORTA, 1884), all of which are Pliocene in age. According to the present study and a previous study by KVAČEK & WALTHER (1991), they show similarities to several East Asian species of the subgenus *Fagus* based on leaf shape, type of secondary venation, number of secondary veins, tooth type, IMR, and cuticle features when available, but not to *F. grandifolia*. TANAI (1974) used the leaf index (length of lamina to width times 100) to distinguish three species groups within modern and fossil *Fagus*. Taken alone, this results in a classification that is at odds with several other morphological characters. It is, however, an informative character provided sufficient variability of a species is known (cf. Table 2).

Among more recent studies on *Fagus*, PALAMAREV & MAI (1998) listed names used in the literature without any critical revision of fossil taxa, and arbitrarily compared them to modern species. In contrast, VAN DER BURGH (2001) used a biometric approach in order to detect changing leaf morphotypes corresponding to stratigraphical units during the Miocene of the Lower Rhine Embayment. The leaf characters measured (length, number of secondary veins, leaf shape), however, may be suitable to detect variation among populations (see DENK, 1999a, b) but are very critical when using a biostratigraphical approach.

More holistic approaches were those by KVAČEK & WALTHER (1989, 1991), and particularly by ZETTER (1984). These studies were similar in concept to the present study but focused on geographically limited areas in Germany/Czech Republic, and Austria, respectively. KVAČEK & WALTHER (1989) recognized a single polymorphic species from the Oligocene to the Pliocene of Central Europe, *F. attenuata*, but later (1991) split this taxon into four different species based mainly on minor differences in epidermal structures. Whereas the oldest of these species, *F. saxonica*, is considered part of a much more widespread European-Asian species *F. castaneifolia* in the present study, the other three species, *F. menzelii, F. silesiaca,* and *F. kraeuselii* are considered conspecific, and synonyms to *F. haidingeri*, because they represent morphotypes that recur at several times and at several places from Europe to Azerbaijan and are not ascribable to different species by means of diagnostic morphological characters/character sets. *Fagus menzelii* has recently been considered a synonym of *F. silesiaca* (WOROBIEC, 2000).

ZETTER (1984) ascribed Early to early Middle Miocene *Fagus* leaves of Austria to *F. attenuata* and Late Miocene specimens to *F. haidingeri*, pointing out the similarities of the latter to East Asian species, such as *F. lucida* and *F. longipetiolata*. This corresponds to the two species of *Fagus* for the Cenozoic of Central Europe recognized here, with a major split occurring between the Early Miocene and the Middle Miocene.

The species concept adopted for the present study relies to a great extent on a phylogenetic framework obtained from extensive molecular and morphological studies, yielding information on the evolutionary mode of the genus (progressive versus conservative), and on major splits within the genus. Both molecular studies (STANFORD, 1998; DENK et al., 2002; GRIMM et al., unpublished data) and morphological studies (DENK, 2003) suggest a conspicuously conservative mode of evolution for *Fagus*, i.e. the majority of species of the subgenus *Fagus* seems to have diversified very late in the Cenozoic. This is reflected by a high amount of ITS polymorphism and by the enormous variability of vegetative characters within and between modern species of *Fagus*. Based on this, it is assumed that fossil species are as variable as modern ones and possibly even more. In addition, it is assumed that fossil species were widespread as are the modern *F. sylvatica, F. longipetiolata, F. crenata,* and *F. grandifolia* - and not restricted to small and/or disrupted areas such as *F. chienii* and *F. hayatae*. Therefore, the present concept runs the risk of overlooking geographically very restricted species that could not possibly be recognized as distinct species in the fossil record. On the other hand, there is no morphological evidence for the presence of several distinct species, for example in the Late Oligocene/Early Miocene of Europe and Central Asia, which would make a “many-species” concept much more complicated and less parsimonious than the “one-species” concept adopted here. Therefore, various very narrow species concepts applied to *Fagus* in previous studies (e.g., ANDREÁNSZKY, 1959; KVAČEK & WALTHER, 1991; BRAMBILLA & GALLO, 2002) appear to be inadequate for this genus.

4.2 Comparison to fossils from the Cenozoic of East Asia and North America (Fig. 16)

Earliest fossils of *Fagus* are from the Middle Eocene of western North America (Washington, British Columbia, PIGG & WEHR, 2002; [1] Fig. 16). These are a few cupule and nut specimens that lack all the apomorphies characteristic of the subgenus *Engleriana*, and as such strongly resemble most of the members of the subgenus *Fagus*. The cupule is 1.5 cm long, with a stout, short (~1 cm) peduncle, and no connecting-piece. Spine-like appendages are short, and the nut is prominently winged along the entire length of the edges, around 1.5 cm long. Specimens resemble the modern North American *F. grandifolia*. From the Late Eocene, leaves from Kamchatka have been described as *F. napanensis* (FOTJANOVA, 1982; BUDANTSEV, 1997; [2] Fig. 16). Lacking epidermal structures and associated cupules/nuts they cannot be ascribed to a modern subgenus of *Fagus*, but clearly do belong to *Fagus* based on the course and arrangement of secondary veins, the semi/ pseudocraspedodromous secondary venation, and the eglandular non-spinose teeth, in connection with patterns of tertiary and higher-order venation.

The focus of this study lies on fossils from western Eurasia. Due to the concept adopted for *F. castaneifolia* the range of this Late Paleogene species clearly extends to Central Asia (eastern Kazakhstan). Central Asian specimens of *F. castaneifolia* have previously been ascribed to *F. antipofii* (e.g., ZHILIN, 1974; ILJINSKAJA, 1982). Originally, the range of this species was assumed to cover an area from Central Asia to Sakhalin and Kamchatka to Alaska (HEER, 1858, 1869, 1878a, b). CHELEBAEVA (1980) recognized that specimens from the Middle Miocene of Kamchatka were fundamentally different from Central Asian specimens of *F. antipofii* and assigned them to a new species *F. evenensis* ([7] Fig. 16). This was based on the very densely spaced secondary and tertiary veins in *F. evenensis*. Here included were also Early Miocene specimens from Sakhalin previously assigned to *F. antipofii*. Later, FOTJANOVA (1988) established another species, *F. salnikovii* based on Late Oligocene to late Early Miocene specimens from Sakhalin, Japan, and Korea, which she distinguished from *F. antipofii* by their partly very large leaves (to > 20 cm), the high length/width ratio of the leaves, and the pseudocraspedodromous venation. *Fagus evenensis* may belong to a lineage that leads to the modern subgenus *Engleriana*. This is based on the densely spaced tertiary veins as argued by CHELEBAEVA (1980, 1982), and is further substantiated by the leaf shape (narrow-obovate with broad obtuse base, or broad ovate-elliptic with cordate base) and the type of secondary venation, dentation, and IMR (pseudocraspedodromous, entire margined or blunt-triangular teeth, straight IMR), which are identical to some leaves of modern *F. engleriana* (pers. obs.). In addition, some of the leaves of *F. evenensis* examined (Vernadsky State Geological Museum, Moscow) have broad triangular teeth with a sharp acuminate apex. Another species from the Early Oligocene of Kamchatka, *F. irvajamensis* (CHELEBAEVA, 1980; [6] Fig. 16) cannot be assigned to a modern subgenus of *Fagus*. Moreover, the irregularly spaced, often camptodromous and fairly curved secondary veins make it impossible to ascribe this species with certainty to *Fagus* (pers. obs.). Also the subgeneric affinities of specimens described from the Early Oligocene of Japan (*F. uemurae*, *"F." kitamiensis*, TANAI, 1995; [4, 5] Fig. 16) are enigmatic. *Fagus uemurae* was established on the basis of eight small (≤ 6 cm) leaves with very densely spaced secondary (13 to 15 pairs) and tertiary veins (12 to 14 per cm) and inconspicuously denticulate margin. *"Fagus" kitamiensis*, based on seven larger (to 11 cm) leaves, is similar to *F. uemurae* but has conspicuous narrowly triangular teeth, which made Tanai uncertain whether to include it within *Fagus* or not. In principle, such teeth are also found in other Cenozoic *Fagus* (*F. pacifica, F. castaneifolia*, and a few leaves of *F. evenensis*). The overall appearance of these specimens is similar to *F. castaneifolia* (long elliptic to ovate-elliptic leaves with high numbers of secondary veins, straight to concave IMR and sharp teeth, or theeth inconspicuous). The holotype of *"F." kitamiensis* is strikingly similar to the modern Chinese *F. longipetiolata* by its trullate leaf shape and long petiole. However, the very densely spaced secondary veins and the high number of tertiary veins per cm (even in large "shade"-leaves) make it impossible to ascribe *F. kitamiensis* to a modern subgenus without evidence from cupules and nuts. The same is true for few badly preserved specimens from the Late Eocene/Oligocene of China (*Fagus* sp. 1 and sp. 2, LIU et al., 1996).

Fagus pacifica CHANEY 1927 ([3] Fig. 16) from the Early Oligocene of western North America (CHANEY, 1927; MAYER & MANCHESTER, 1997) clearly shows the plesiomorphic characteristics of the subgenus *Fagus*, based on cupule/nut features and leaf morphology (secondary venation, tooth type, IMR), and appears to be closely related to *F. castaneifolia. Fagus pacifica* is represented by rather small leaves that may be sun-leaves and by cupules and nuts. Characters to distinguish it from *F. castaneifolia* are the presence of subsidiary teeth, and perhaps the higher density of tertiary veins (10 to 13 per cm in "sun"-leaves), and the absence of the thickened connecting-piece (DENK & MELLER, 2001) between peduncle and cupule. While cupule and nut features are identical to the modern North American *F. grandifolia*, subsidiary teeth are very rare in the modern species and the densely spaced tertiary veins are found in Mexican populations of *F. grandifolia*, but not in eastern North American ones (see Table 2). The Early to Middle Miocene *F. washoensis* LA MOTTE 1936 (Washington to California) comprises medium-sized (up to 11 cm long) oblong-ovate leaves with narrow-triangular teeth and craspedodromous secondary venation. It has been compared to the modern Chinese *F. longipetiolata* by LA MOTTE (1936). Smaller (to 7 cm long) leaves from the Late Miocene, previously ascribed to *F. washoensis*, were later assigned to another species, *F. idahoensis* CHANEY & AXELROD 1959, because of differences in size and shape. Cupules associated with these leaves are identical to those of *F. pacifica* (absence of connecting-piece, see above), and to modern *F. grandifolia*. Based on observations of modern species the differences in leaf gross-morphology between these two fossil species could well be within the range of variability of a single species, and even CHANEY & AXELROD (1959) in their original paper on *F. idahoensis* mentioned the possibility that it could represent an ecotype of *F. washoensis*. These two taxa appear to represent a lineage leading to the modern *F. grandifolia* and differ from *F. pacifica* merely by leaf characters (no subsidiary teeth, leaf shape), while cupules are identical.

Among the scarce fossil remains described from China the Oligocene *F. galbanifolia* GUO from northeastern China (LIU et al., 1996), and the specimens ascribed to *F. koraica* by GUO & ZHANG (2002) resemble *F. pacifica* in leaf shape, size, type of secondary venation, and tooth type and IMR, whereas *F. "florinii"* (*sensu* GUO & ZHANG, 2002), represented by few small (3 cm long) leaves, is difficult to assign to a modern or fossil species.

Leaf fossils from the Neogene that can be ascribed with some certainty to the subgenus *Engleriana* are from the Late Miocene, Pliocene, and Pleistocene of Japan (*F. protojaponica* K. SUZUKI, 1959; TANAI & SUZUKI, 1965; TANAI, 1974; [10] Fig. 16; *F. japonica* MAXIM., ENDÔ, 1940). These are leaves that are indistinguishable from modern members of the subgenus *Engleriana* by their leaf shape, and number and type of secondary and tertiary veins.

From the Neogene of China, Japan, and Korea several species belonging to the subgenus *Fagus* have been reported, but comparative studies on a wider geographical scale are missing. Interestingly, China is very poor in fossil *Fagus* (LIU et al., 1996), except for the northeastern part of China facing the Pacific, whereas Korea and particularly Japan are rich in fossils. From Korea, *F. protolongipetiolata, F. koraica,* and *F. uotanii* (HUZIOKA, 1951, 1972) were distinguished on the basis of minor differences in size. They have trullate leaves similar to modern *F. longipetiolata* and *F. lucida*. From Japan *F. florinii* HUZIOKA & TAKAHASHI 1973 and *F. palaeocrenata* OKUTSU 1955 were described. Interestingly, all these leaf forms can be found among specimens belonging to *F. stuxbergii* (NATHORST) TANAI (TANAI, 1976; [8] Fig. 16) from the Pliocene of Japan and should perhaps be included within this species. *Fagus stuxbergii*, represented by hundreds of leaves, is similar to *F. haidingeri* and clearly belongs to the subgenus *Fagus*. It differs from *F. haidingeri* by the abundant occurrence of attenuate leaf apices and resembles modern *F. hayatae, F. crenata,* and *F. lucida/chienii* based on leaf shape, type of secondary venation, and tooth type. Whereas ILJINSKAJA (1982) reported widely spaced (4 / 1 cm) anastomosing tertiary veins for *F. stuxbergii*, the specimens figured in TANAI (1976) show 8 to 14 tertiaries, corresponding to values observed for *F. haidingeri*. Like in European localities entire-margined "*F. crenata*"-like leaves co-occur with dentate ones.

From the Miocene of eastern Kazakhstan distinct leaves, cupules, and nuts were described by KORNILOVA & RAYUSHKINA (1968) as *F. altaensis* ([9] Fig. 16) and *F.* sp. 1 and sp. 2, respectively. According to ILJINSKAJA (1982) both leaves and cupules and nuts display close similarities to the modern Chinese *F. lucida*, which is distinct from all other species of the subgenus *Fagus* by its scale-like cupule appendages and unwinged nuts that are conspicuously longer than the cupule valves (DENK & MELLER, 2001). Whereas the imprint of a cupule figured in RAYUSHKINA (1979) superficially resembles *F. lucida*, the nuts found together with the cupule are shorter than the valves and have winged upper edges according to RAYUSHKINA (1979). Associated with leaves having hooked teeth and cordate leaf bases *F. altaensis* appears to be a distinct type in the Miocene of eastern Kazakhstan. From the late Middle Miocene/Late Miocene of northeastern China LENG (2000) described five species based on leaf compressions without cuticles. Most of the specimens were assigned to two species, *F. altaensis* and *F. antipofii*. The remaining species (*F. florinii, F. silesiaca, F.* sp.) are based on single or very few specimens and could perhaps be sun-leaves of *F. antipofii*. They differ from the latter only by higher density of tertiary veins. Another Early to Late Miocene species, *F. chankaica* ALEXEENKO (in KRASSILOV & ALEXEENKO, 1977), was described from the Russian Far East based on relatively large (6-12 cm) ovate-elliptic leaves with sharp triangular teeth and straight IMR. They have been compared to the modern *F. grandifolia* by ILJINSKAJA (1982).

There is clearly a need for a monographic study of East Asian Cenozoic *Fagus*. To trace the origin of *Engleriana* it would be interesting to evaluate the relationship between the Early Oligocene Japanese *F. uemurae/kitamiensis* and the Early to Middle Miocene *F. evenensis*. Particularly, it would be interesting to trace the appearance of subgenus *Engleriana*-like pollen (small with very long colpi). Furthermore, the relation of *F. castaneifolia* to the Middle/Late Miocene specimens of northeastern China (*F. antipofii,* LENG, 2000) ought to be clarified. The fact that *F. altaensis* from the Miocene of eastern Kazakhstan cannot be compared to any modern species of *Fagus* could be related to the disruption of the continuous Eurasian range of *Fagus* in the course of the Miocene. While the western Eurasian populations gave rise to *F. gussonii* and *F. haidingeri*, the eastern Asian ones evolved into *F. stuxbergii* and similar types, both leading to modern European/Asian Minor and East Asian species. In contrast, Central Asia became unsuitable for the genus *Fagus*.

4.3 Conclusions

4.3.1 Systematic (alpha-taxonomical) studies of Cenozoic plant taxa require labor-intensive and time-consuming studies of modern taxa to establish interspecific and intraspecific morphological variability. Ideally, at least some species ought to be studied in the field in addition to herbarium studies (compare KNOBLOCH & VELITZELOS, 1986). Morphological variability encountered in modern taxa can be a guideline when assessing variability and species delimitation within and between fossil taxa. Species delimitation based on morphological characters is highly taxon-dependent. In case of *Fagus* intraspecific leaf variability is conspicuously high and markedly distinct morphotypes can be distinguished within a single species. Therefore, a wide species concept appears to be required when dealing with *Fagus* from the Cenozoic.

4.3.2 Modern phylogenetic studies based on morphology and molecular markers may yield crucial information about the mode of evolution in different plant taxa (genera), i.e. conservative versus progressive (or conserved versus variable in terms of molecular marker regions). The evolutionary mode is taxon-specific. For modern *Fagus* morphological and molecular studies show a conspicuously large amount of intraspecific variability and ancient polymorphisms (DENK et al., 2002; DENK, 2003; GRIMM, 2003). This points to low levels of species diversification, and, for members of the subgenus *Fagus*, to late differentiation in the course of the Cenozoic. This is perfectly in line with patterns of leaf morphology encountered in the Neogene *Fagus haidingeri*, displaying a mosaic of features found in (closely related) modern species

4.3.3 Monographic studies of Cenozoic plant taxa integrating paleobotanical and recent botanical approaches have wider implications. They are essential for evaluating phylogeographical studies (see, e.g., MANCHESTER & TIFFNEY, 2001), and paleoclimate reconstructions based on "nearest living relatives". Moreover, such studies would be the prerequisite for reliable estimates on past biodiversity.

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Tables on the next pages

SHEN1992			Distribution
Subgenus *Engleriana*		*Fagus engleriana* SEEMEN (incl. *F. multinervis* NAKAI)	China, South Korea
		Fagus japonica MAXIM.	Japan
		Fagus okamotoi SHEN	Japan*
Subgenus *Fagus*	a	*Fagus longipetiolata* SEEMEN	China
		Fagus brevipetiolata HU	China*
		Fagus bijiensis C.F. WEI & Y.T. CHANG	Western China**
		Fagus tientaiensis T.N. LIOU	Eastern China**
	b	*Fagus lucida* REHDER & WILSON	China
		Fagus chienii CHENG	Western China**
		Fagus hayatae PALIBIN (incl. *F. pashanica* C.C. YANG)	China mainland, Taiwan
		Fagus crenata BLUME	Japan
	c	*Fagus sylvatica* L. (incl. *F. orientalis* LIPSKY, *F. moesiaca* (MALY) CZECZ.)	Europe, southwestern Asia
	d	*Fagus grandifolia* EHRH. (incl. *F. mexicana* MARTINEZ)	Eastern North America, Mexico

Note. a sect. *Longipetiolata* , b sect. *Lucida* , c sect. *Fagus* , d sect. *Grandifolia*
* known from few localities, ** known from a single one locality
Species in normal script are not recognized as distinct species in the present study.
No subspecies are indicated.

Table 1: Most recent classification of *Fagus* by SHEN (1992).

	Leaf length (cm)	Leaf index (length to width x 100)	Apex	No. of secondary veins / 5 cm[a]	Max. no. of secondary veins
F. engleriana SEEMEN	(6) 8-12 (15)	(160-) 215 (-260)	(acute) to acuminate	7-10 (12)	20
F. japonica MAXIM.	(6) 10-12 (15)	(180-) 210 (-250)	(acute) to acuminate	7-10 (11)	20
F. okamotoi SHEN	6-8 (9)	(210-) 230 (-270)	Acute	7-10	15
F. longipetiolata SEEMEN	8-12 (16)	(200-) 260 (-320)	Acuminate to (acute), acumen long and narrow	6-8	18
F. lucida REHDER & WILSON	(5) 6-9 (12)	(175-) 245 (-295)	Acuminate to acute, acumen long and narrow	6-8	15
F. chienii CHENG	4-9	(195-) 230 (-270)	Acute	6-8	12
F. hayatae PALIBIN	(2) 3-8 (9)	(180-) 215 (-286)	Acuminate, acumen short or long	7-10	14
F. crenata BLUME	(3) 6-10 (12)	(150-) 190 (-240)	Acute to acuminate	7-9	12
F. sylvatica L.	(4) 6-10 (18)	(140-) 172 (-250)	Acute to acuminate (acumen blunt to acute)	5-9	17
F. grandifolia EHRH.	(5) 7-14 (20)	(200-) 250 (-290)	Acuminate to acute, acumen long and narrow	7-10	22

Note. [a] 100+ measurements

[b] P = pseudocraspedodromous, S = semicraspedodromous, C = craspedodromous, B = brochidodromous

[c] 0 = teeth normally absent, 1-4 refers to tooth types 1 to 4 described in the text.

[d] P, W = papillae and wax ornamentation on lower epidermis, A = anomocytic stomata, S = small stomata (for details see ZETTER 1984, KVAČEK & WALTHER 1991, DENK 2003)

Table 2: Comparative leaf morphology of extant species of *Fagus*.

Type of secondary venation[b]	Intersecondary margin region	Tooth type[c]	Subsidiary teeth	No. of tertiary veins / cm (this study)	No. of tertiary veins / cm (ZETTER 1984)	No. of tertiary veins / cm (KVAČEK & WALTHER 1991)	P, W[d]	A[d]	S[d]
B & P	(straight) to convex	0	No	13-14 shade, 13-18 sun	9-13	10-12	+	+	+
B & P	(straight) to convex	0	No	13-14 shade, 13-18 sun	10-13	10	+	+	+
B & P	Straight	0	No	14 sun	-	-	+	+	+
P & S & C	Straight to convex	0 & 1 (& 2 & 3) ((& 4))	No	8-9 shade, 11 sun	Up to 8	7	+	-	-
S & C	Straight to convex	2 (& 3)	Yes	9-11	5-7	8	-	-	-
P & S & C	Convex	0 & 2	No	8-10	-	-	-	-	-
S & C	Convex	3	Yes	9-11 shade, 12-15 sun	5-7	11 ssp. pash., 9 ssp. hay.	-	-	+
B & P	Convex	0	No	6-9 shade, 12-14 sun	5-8	10	-	-	-
B & P & S	Straight to convex to concave	0 (& 4)	No	6 shade, 13-14 sun	5-7	9	-	-	-
P & S & C	Straight to concave to (convex)	4	No	7-9 eastern N America, 8-13 Mexico	6-8 eastern N America, 6-8 Mexico	11 eastern N America, 15 Mexico	-	+	+

Table 2 (continued)

	Long ovate (trullate)	Elliptic (oblong)	Rhombic	Obovate (obtrullate)
F. engleriana SEEMEN	-	+	+	+
F. japonica MAXIM.	-	+	+	+
F. okamotoi SHEN	-	+	+	+
F. longipetiolata SEEMEN	+	+	-	-
F. lucida REHDER & WILSON	+	+	-	-
F. chienii CHENG	+	+	-	-
F. hayatae PALIBIN	+	+	-	-
F. crenata BLUME	(+)	+	+	+
F. sylvatica L.	-	+	+	+
F. grandifolia EHRH.	+	+	+	+
F. castaneifolia UNGER	+	+	-	-
F. gussonii MASS.	+	+	+	+
F. haidingeri KOV.	+	+	+	-

Table 3: Leaf shape in shade leaves and leaves of vegetative shoots

	Length (max., cm)	Leaf index (length to width x 100)	No. of second. veins (max.)	No. of tertiary veins/cm	Type of secondary venation[f]	Tooth type[g]	Intersecondary margin region	Subsidiary teeth
F. castaneifolia UNGER	14.5	(180-) 250 (-300)	20	4 to 5[a], 8 to 10[b]	C, S, (P)	(0,) 1, 2, 4	Straight to concave	Absent
F. gussonii MASS.	14	(150-) 200 (-250)	16	9 to 12	P, S, (C)	0, 1	Straight to convex	Absent
F. haidingeri KOV.	12	(155-) 210 (-270)	14	9 to 15[c], 11 to 14[d], 10[e]	S, C, P	0, 1, 2, 3, (4)	Convex to straight	Present

[a] ILJINSKAJA 1982: *F. antipofii* (large leaves), [b] KVAČEK & WALTHER 1991: *F. saxonica*. [c] KVAČEK & WALTHER 1991: *F. menzelii, F. kraeuselii*. [d] WALTHER & ZASTAWNIAK 1991: *F. silesiaca*. [e] ILJINSKAJA 1982: *F. attenuata*.

[f] P=pseudocraspedodromous, S=semicraspedodromous, C=craspedodromous.

[g] Teeth may also be absent (0), see text and Table 2 for explanation of tooth types 1 to 4.

Table 3a: Diagnostic features of the three leaf-morphotaxa of *Fagus* in the Cenocoic of Europe and western Eurasia.

Present study:	*F. castaneifolia*	*F. gussonii*	*F. haidingeri*	*F. haidingeri*	*F. haidingeri*	*F. haidingeri*	*F. haidingeri*
Previous names:	*F. saxonica*	*F. gussonii*	*F. menzelii*	*F. silesiaca*	*F. silesiaca* var. *gozdnicensis*	*F. attenuata*	*F. kraeuselii*
	KVAČEK & WALTHER 1991	KVAČEK, VELITZELOS & VELITZELOS 2002	KVAČEK & WALTHER 1992	WALTHER & ZASTAWNIAK 1991	ŁANCUCKA-ŚRODONIOWA et al. 1992	HUMMEL 1983	KVAČEK & WALTHER 1992
	Late Oligocene	Late Miocene	Middle Miocene	Late Miocene	Late Miocene	Early Pliocene	Late Pliocene
Upper epidermis							
Cell shape	Polygonal, finely undulate	-	Polygonal, finely undulate	Isodiametric to rectangular; rounded to undulate-walled	Polygonal, undulate anticlines	Undulate anticlines	Finely undulate
Size of cells (µm)	15 - 40	-	10 - 40	25 - 40	30 - 35	25 - 45	17 - 30 - 47
Trichome bases	-	-	-	Bases of eglandular trichomes rarely on veinlets	-	-	-
Lower epidermis							
Anticlines	Curved to finely undulate	Slightly curved	Finely undulate	Rounded to undulate	Undulate	-	Straight to rounded
Size of cells (µm)	-	-	17 - 30	Slightly smaller than on upper epidermis	Ca. 15 x 40	18 - 25 (-30)	13 - 30
Trichomes	Bases of eglandular and glandular trichomes	-	Bases of eglandular and glandular trichomes	Bases of eglandular and glandular trichomes	Bases of eglandular and glandular trichomes	Bases of eglandular and glandular trichomes	Bases of eglandular and glandular trichomes
Arrangement of subsidiary cells	Incomplete cyclocytic (to anomocytic)	Anomocytic to incompletely cyclocytic-actinocytic	Incomplete cyclocytic (to anomocytic, to actinocytic)	Imperfect cyclocytic	Cyclocytic to incomplete cyclocytic (to anomocytic)	Cyclocytic	Cyclocytic to incomplete cyclocytic (to actinocytic and anomocytic)
No. and shape of subsidiary cells	Narrow to isodiametric	Narrow	3 to 5 narrow subsidiary cells	3 to 5 narrow subsidiary cells	Narrow, to radially arranged	5 to 6 narrow subsidiary cells	3 to 5 narrow subsidiary cells
Stomata (l x w; µm)	12 - 26 x 12 - 23	20 - 27 x 18	14 - 24 x 12 - 28	15 - 22 x 12 - 21	17 - 26 x 19 - 26	18 - 24 x 16 - 20	18 - 32 x 15 - 27
Stomata length (mean)	14-16	-	18-22	18-20	-	-	18-22

Table 4: Leaf epidermal characteristics of the three leaf-morphotaxa of *Fagus*occurring in the Cenocoic of Europe and western Eurasia.

Reference	Locality	Age	Previous name	Revised name
MASSALONGO & SCARABELLI, 1859	Senigallia, Marche	Messinian	*F. gussonii*	***F. gussonii***
SORDELLI, 1896	Montescano, Pavia, Lombardy	1st evaporitic phase of the Messinian	*F. antipofii*, *F. marsilii*	"Hybrid zone" between *F. haidingeri* /*F. gussonii* ?
BERGER, 1957	Gabbro, Tuscany	Messinian	*F. attenuata*, *F. marsilii*	"Hybrid zone" between *F. haidingeri* /*F. gussonii* ?
BRAMBILLA & GALLO, 2002	Nizza Monferrato, Piedmont	1st evaporitic phase of the Messinian	*F. antipofii*, *F. haidingeri*, *F. latissima*	"Hybrid zone" between *F. haidingeri* /*F. gussonii* ?
This study	Castagnito, Scaparoni d'Alba; Piedmont	1st evaporitic phase of the Messinian	-	"Hybrid zone" between *F. haidingeri* /*F. gussonii* ?
FISCHER & BUTZMANN, 2000	Meleto, Tuscany	Middle Pliocene	*F. attenuata*, *F. haidingeri*	***F. haidingeri***
MARTINETTO, 2003	Asti, Piedmont	Latest Early Pliocene to earliest Middle Pliocene	*F. pliocenica*	***F. haidingeri***
This study	Valmanera, Asti, Piedmont	Latest Early Pliocene to earliest Middle Pliocene	-	***F. haidingeri***

Table 5: Distribution and stratigraphy of some Italian occurrences of *Fagus* illustrating possible hybrid zones between *F. gussonii* and *F. haidingeri* in the Messinian.

References

ANDREÁNSZKY, G. (1959) Die Flora der sarmatischen Stufe in Ungarn. Akadémiai Kiadó, Budapest, 360 pp., 68 plates.

BARRÓN, E., DIÉGUEZ, C. (1994) Neogene species of the genus *Fagus* L. from La Cerdaña (Lerida, Spain). Taxonomic conclusions and phylogenetic considerations. Ann. Jard. Bot. Madrid 52 (1): 21-32.

BERGER, W. (1957) Untersuchungen an der obermiozänen (Sarmatischen) Flora von Gabbro (Monti Livornesi) in der Toskana. Palaeontographica Italica 51: 1-96, 25 plates.

BRAMBILLA, G., GALLO, L. M. (2002) Analisi stratigraphica e paleobotanica della successione messiniana di Bric Santa Margherita (Nizza Monferrato, Asti, Italia NW). Boll. Mus. Reg. Sci. Nat. Torino 19 (1): 191-283, 15 plates.

BUDANTSEV, L. Y. (1997) Late Eocene flora of western Kamchatka. Russian Academy of Sciences. Proceedings of Komarov Botanical Institute 19, Saint-Petersburg, 115 pp., 77 plates.

CHANEY, R. W. (1927) Geology and Palaeontology of the Crooked River basin, with special reference to the Bridge Creek flora. In: KELLOG, R., MERRIAM, J. C., STOCK, C., CHANEY, R. W., MASON, H. L.: Additions to the palaeontology of the Pacific coast and Great Basin regions of North America. Carnegie Institution of Washington, Publication 346: 45-138, 20 plates.

CHANEY, R. W., AXELROD, D. I. (1959) Miocene floras of the Columbia Plateau. Carnegie Institution of Washington, Publication 617, 237 pp., 44 plates.

CHELEBAEVA, A. I. (1980) New Cainozoic species of *Fagus* (Fagaceae) from Kamchatka and the significance of tertiary venation for the diagnostics of *Fagus* species. Bot. J. 65 (1): 3-12, plates 3-6.

CHELEBAEVA, A. I. (1982) *Fagus irvajamensis* Cheleb., *Fagus evenensis* Cheleb. In: TAKHTAJAN, A. L. (ed): Magnoliophyta Fossilia SSSR vol 2: 63-66. Leningrad, 216 pp., 172 plates.

DENK, T. (1999a) The taxonomy of *Fagus* in western Eurasia, 1: *Fagus sylvatica* subsp. *orientalis* (=*Fagus orientalis*). Feddes Repert. 110 (1-2): 177-200, 9 plates.

DENK, T. (1999b) The taxonomy of *Fagus* in western Eurasia, 2: *Fagus sylvatica* subsp. *sylvatica*. Feddes Repert. 110 (5-6): 381-412, 14 plates.

DENK, T., MELLER, B. (2001) The systematic significance of the cupule/nut complex in living and fossil *Fagus*. Int. J. Plant Sci. 162 (4): 869-897.

DENK, T., GRIMM, G., STÖGERER, K., LANGER, M., HEMLEBEN, V. (2002) Differentiation of *Fagus* in Europe and southwestern Asia – evidence from rDNA (ITS1 and ITS2) sequences and morphological data. Plant Syst. Evol. 232: 213-236.

DENK, T. (2002) Revision of *Fagus* cupules described in Magnoliophyta Fossilis USSR. Feddes Repert. 113 (3-4): 193-210, 7 plates.

DENK, T. (2003) Phylogeny of *Fagus* L. (Fagaceae) based on morphological data. Plant Syst. Evol. 240: 55-81.

DJORDJEVIC-MILUTINOVIC, D., DULIC, I. A., PANTIC, N. K. (2002) Preliminary reconstruction of Lower Miocene vegetation of Berane Basin (Montenegro, Yugoslavia). 6th European Paleobotany-Palynology Conference, August 29-September 2, 2002, Athens, Greece, Abstract volume: 134.

ENDÔ, S. (1940) A Pleistocene flora from Siobara, Japan. Science Reports of the Tôhoku Imperial University, second series (Geology) 21 (1): 47-80, 9 plates.

ERDEI, B., YAVUZ, N., AKGUN, F., HABLY, L. (2002) Some data to the Miocene flora of western Turkey. 6th European Paleobotany-Palynology Conference, August 29-September 2, 2002, Athens, Greece, Abstract volume: 79-80.

FISCHER, T. C., BUTZMANN, R. (2000) Die neogene Flora von Meleto (Valdarno, Italien) Paläobotanik, Paläoökologie und Paläoklima. Flora Tertiaria Mediterranea 5 (6): 1-187, 29 plates.

FOTJANOVA, L. I. (1982) *Fagus napanensis* Fotjan. sp. nov. In: TAKHTAJAN, A. L. (ed.) Magnoliophyta Fossilia SSSR vol. 2: 64. Leningrad, 216 pp., 172 plates.

FOTJANOVA, L. I. (1988) The Flora of the Far East at the boundary of Palaeogene and Neogene (by the example of Sakhalin and Kamchatka). Nauka, Moscow.

FRIEDRICH, W. L., SÍMONARSON, L. A., HEIE O. E. (1972) Steingervingar í Millilögum í Mókollsdal. Náttúrufræðingnum 42: 4-17.

GIVULESCU, R., GHIURCA, V. (1969) Flora pliocenă de la Chiuzbaia (Maramureş) cu un studiu geologic introductiv. Memorii 10: 1-81, 17 plates.

GOEPPERT, H. R. (1855) Die tertiäre Flora von Schossnitz in Schlesien. Heyn'sche Buchhandlung (E. Remer), Görlitz, 52 pp., 26 plates.

GORTEMAKER, R. E. (1986) A method to identify pollen of some recent and fossil species of *Fagus* L. (Fagaceae). Rev. Palaeobot. Palynol. 47 (1-2): 263-292.

GRIMM, G. W. (2003) Tracing the mode and speed of intrageneric evolution – A phylogenetic case study on genus *Acer* L. (Aceraceae) and genus *Fagus* L. (Fagaceae) using fossil, morphological, and molecular data. Ph.D. thesis, IfG, Eberhard-Karls-University, Tübingen, Germany, 228 pp.

GRÍMSSON, F., DENK, T., *Fagus* from the Miocene of Iceland: Systematics and biogeographical considerations. Submitted to Review of Palaeobotany and Palynology, 14 plates.

GUO, S.-X., ZHANG, G.-F. (2002) Oligocene Sanhe flora in Longjing county of Jilin, northeast China. Acta Palaeont. Sinica 41 (2): 193-210, 3 plates.

HEER, O. (1858) *Fagus antipofii*. In: ABICH, W. H.: Beiträge zur Paläontologie des asiatischen Russland. Mém. Acad. Sci. St.-Pétersbourg 6 (7): 572.

HEER, O. (1869) Flora fossilis Alaskana. Kgl. Svenska Vet. Akad. Handl. 8 (4): 1-41, 10 plates.

HEER, O. (1878a) Beiträge zur Miocenen Flora von Sachalin. Kgl. Svenska Vet. Akad. Handl. 15 (4): 1-11, 4 plates.

HEER, O. (1878b) Miocene Flora der Insel Sachalin. Mém. Acad. Sci. St.-Pétersbourg 25 (7): 1-61, 15 plates.

HUANG, C., ZHANG, Y., BARTHOLOMEW, B. (1999) Fagaceae. In: WU, Z., RAVEN, P. H. (eds.) Flora of China, Volume 4. Cycadaceae through Fagaceae. Science Press Beijing, Missouri Botanical Garden Press, St. Louis, 464 pp.

HUMMEL, A. (1983) The Pliocene leaf flora from Ruszów near Żary in Lower Silesia, SW Poland. Prace Muz. Ziemi 36: 9-104, 57 plates.

HUZIOKA, K. (1951) Notes on some Tertiary plants from Tyosen (Korea). 2. Trans. Proc. Palaeont. Soc. Japan, 3: 67-74.

HUZIOKA, K. (1972) The Tertiary Floras of Korea. J. Min. Coll. Akita Univ., Ser. A 5 (1): 1-83, 14 plates.

HUZIOKA, K., TAKAHASHI, E. (1973) The Miocene Flora of Shimonoseki, Southwest Honshu, Japan. Bull. Nat. Sci. Mus. 16 (1): 115-148.

ILJINSKAJA, I. A. (1982) *Fagus* L. In: TAKHTAJAN, A. L. (ed.) Magnoliophyta Fossilia SSSR vol. 2: 60-73. Leningrad, 216 pp., 172 plates.

ILJINSKAJA, I. A. (1964) The Tortonian flora of Swoszowice (in Russian). In: TAKHTAJAN, A. L. (ed.) Palaeobotanica V: 113-144, 7 plates. Nauka, Moscow, Leningrad, 240 pp.

KNOBLOCH, E. (1969) Tertiäre Floren von Mähren. Brno, 200 pp., 79 plates.

KNOBLOCH, E. (1971) Die tertiäre Flora von Seussen und Pilgramsreuth (Nordbayern). Erlang. Geol. Abh. 87: 1-26, 4 plates.

KNOBLOCH, E. (1988) Neue Ergebnisse zur Flora aus der Oberen Süßwassermolasse von Aubenham bei Ampfling (Kreis Mühldorf am Inn). Documenta naturae 42: 1-27, 14 plates.

KNOBLOCH, E. (1998) Der pliozäne Laubwald von Willershausen am Harz (Mitteleuropa). Documenta naturae 120: 1-302, 64 plates.

KNOBLOCH, E., VELITZELOS, E. (1986) Die obermiozäne Flora von Likudi bei Elassona/Thessalien, Griechenland. Documenta naturae 29: 5-20, 9 plates.

KOLAKOVSKI, A. A. (1960) On the history of beech in Eurasia. Trudy Moskovskogo Obshchestva Ispytateley Prirody 3: 141-156.

Kolakovski, A. A. (1964) A Pliocene flora of the Kodor River. Georgian Academy of Sciences, Inst. Syst. Bot. Monographs 1: 1-209, 56 plates.

Kolakovski, A. A., Ratiani, N. K. (1967) A Pliocene flora of Malyi Shirak. Trudy Sukhumskogo botanicheskogo sada, vol. 16: 30-71, 11 plates.

Kornilova, V. S., Rayushkina, G. S. (1968) Novyi vid *Fagus altaensis* sp. n. Kornilova et Rayushkina. Biologiya i geografiya 4: 16-17. Alma-Ata.

Kovar-Eder, J. (1982) Eine Blätterflora des Egerien (Ober-Oligozän) aus marinen Sedimenten der zentralen Paratethys im Linzer Raum (Österreich). Beitr. Paläont. Österr. 9: 1-209, 38 plates.

Kovar-Eder, J. (1988) Obermiozäne (Pannone) Floren aus der Molassezone Österreichs. Beitr. Paläont. Österr. 14: 19-121, 12 plates.

Kováts, J. (1856) Fossile Flora von Erdöbénye. Arbeiten geol. Ges. Ungarn, Heft 1, Pesth: 1-37, 7 plates.

Krassilov, V. A., Alexeenko, T. M. (1977) Succession of plant communities in the Paleogene and Neogene of South Primorye. In: Krassilov, V. A. (ed.) Paleobotany in the Far East. Academy of Sciences of the USSR. Far-Eastern Scientific Centre, Institute of Biology and Pedology, pp. 7-18. Vladivostok, 80 pp., 36 plates.

Kryshtofovich, A. N. (1938) The Miocene Flora of Ukraine and its connection through the Urals with the Tertiary Flora of Asia. Zbyrnik prac', prysvyachenyi pam'yati ak. O. V. Fomina. Kyiv, pp. 74-105, 5 plates.

Kryshtofovich, A. N., Baikovskaya, T. I. (1965) Sarmatian Flora of Krynka. Russ. Acad. Sc. Moscow-Leningrad, 135 pp., 39 plates.

Kutuzkina, E. F. (1964) The Sarmatian Flora of Armavir (in Russian). In: Takhtajan, A. L. (ed.) Palaeobotanica V: 145-230, 18 plates. Nauka, Moscow-Leningrad, 240 pp.

Kvaček, Z., Walther, H. (1989) Palaeobotanical studies in Fagaceae of the European Tertiary. Plant Syst. Evol. 162: 213 - 229.

Kvaček, Z., Walther, H. (1991) Revision der mitteleuropäischen Fagaceen nach blattepidermalen Charakteristiken. IV. Teil *Fagus* L. Feddes Repert. 102 (7-8): 471-534, 20 plates.

Kvaček, Z., Velitzelos, D., Velitzelos, E. (2002) Late Miocene Flora of Vegora Macedonia N. Greece. Korali Publications, Athens, 175 pp., 32 plates.

La Motte, R. S. (1936) The Upper Cedarville Flora of northwestern Nevada and adjacent California. In: Oliver, E., La Motte, R. S. Middle Cenozoic floras of western North America, pp. 57-142, 14 plates. Carnegie Institution, Washington, 152 pp.

Łańcucka-Środoniowa, M., Kvaček, Z., Zastawniak, E. (1992) Macroscopic plant remains from the Gozdnica and Gozdnica-Stanislaw localities. In: Zastawniak, E. (ed.)

The younger Tertiary deposits in the Gozdnica Region (SW Poland) in the light of recent palaeobotanical research. Polish Bot. Stud. 3: 17-46, plates 1-26.

LAURENT, L., MARTY, P. (1923) Flore foliaire Pliocène des Argiles de Reuver et des gisements synchroniques voisins (Limbourg Hollandais). Mededeelingen van's Rijks Geologischen Dienst, Ser. B, no. 1, Leiden, 80 pp., 14 plates.

LENG, Q. (2000) Fagaceae from the Miocene Daotaiqiao formation of Huanan, Heilongjiang, China. Acta Palaeont. Sinica 39 (Suppl.): S251-S287, 10 plates.

LIU, Y.-S., MOMOHARA, A., MEI, S.-W. (1996) A revision on the Chinese megafossils of *Fagus* (Fagaceae). Jap. Journ. Bot. 71 (2): 168 - 177.

MÄDLER, K. (1939) Die Pliozäne Flora von Frankfurt am Main. Abh. Senckenberg naturforsch. Ges. 446: 1-202, 13 plates.

MÄDLER, K., STEFFENS, P. (1979) Neue Blattfloren aus dem Oligozän, Neogen und Pleistozän der Türkei. Geol. Jb., B33: 3-33, 6 plates.

MAI, H. D., WALTHER, H. (1988) Die Pliozänen Floren von Thüringen, Deutsche Demokratische Republik. Quartärpaläont. 7: 55-297, 41 plates.

MAI, H. D., WALTHER, H. (1991) Die oligozänen und untermiozänen Floren Nordwest-Sachsens und des Bitterfelder Raumes. Abh. Staatl. Museum Min. Geol. Dresden 38: 1-201.

MAI, H. D., VELITZELOS, E. (1997) Paläokarpologische Beiträge zur jungtertiären Flora von Vegora (Nordgriechenland). Feddes Repert. 108 (7-8): 507-526, 7 plates.

MANCHESTER, S. R., TIFFNEY, B. H. (2001) Integration of paleobotanical and neobotanical data in the assessment of phytogeographic history of holarctic angiosperm clades. Int. J. Plant Sci. 162 (6Suppl.): S19-S27.

MANOS, P. S:, STANFORD, A. M. (2001) The historical biogeography of Fagaceae: Tracking the Tertiary history of temperate and subtropical forests of the Northern Hemisphere. Int. J. Plant Sci. 162 (6Suppl.): S77-S93.

MARTINETTO, E. (2003) Leaves of terrestrial plants from the shallow marine and transitional Pliocene of Asti (Piedmont, NW Italy). Bollettino Società Paleontologica Italiana 42 (1): 75-116.

MASSALONGO, A. (1853) Descrizione di alcune plante fossili terziarie dell'Italia meridionale. Nuovi Annali delle scienze nat., Ser. 3, Vol. 8: 1-9, 2 plates.

MASSALONGO, A. (1858) Synopsis florae fossilis Senogalliensis. Verona, Italy, 138 pp.

MASSALONGO, A., SCARABELLI, G. (1859) Studii sulla flora fossile e geologia stratigrafica del Senigalliese. Imola, Italy, 504 pp., 45 plates.

MENZEL, P. (1906) Über die Flora der Senftenberger Braunkohlenablagerungen. Abhandlungen der Königlich Preussischen Geologischen Landesanstalt und Bergakademie, Neue Folge, Heft 46. Berlin, 154 pp., 7 plates.

MEYER, H. W., MANCHESTER, S. R. (1997) The Oligcene Bridge Creek Flora of the John Day Formation, Oregon. Univ. California Publ. 141: 1-195, 75 plates.

NATHORST, A. G. (1883) Contribution à la flore fossile du Japon. Kgl. Svenska Vet. Akad. Handl. 20: 3-92, 16 plates.

OKUTSU, H. (1955) On the stratigraphy and palaeontology of Cenozoic plant beds of Sendai area. Sci. Rep. Tohoku Univ., Ser. 2, 26: 1-114, 8 plates.

PALAMAREV, E., MAI, H. D. (1997) Die paläogenen Fagaceae in Europa: Artenvielfalt und Leitlinien ihrer Entwicklungsgeschichte. Acta Palaeobot. 38: 227-299, 12 plates.

PALIBIN, I. V. (1939) Materials to the Tertiary flora of Armenia. To the president of the Academy of Sciences of the USSR the academician Vladimir Leontyevich Komarov to his seventieth anniversary and to the forty-fifth anniversary of his scientific work, pp. 607-630. Leningrad.

PIGG, K. B., WEHR, W. C. (2002) Tertiary flowers, fruits, and seeds of Washington State and adjacent areas – Part III. Washington Geology 30 (3/4): 3-16.

RAYUSHKINA, G. S., KORNILOVA, V. S. (1979) The Oligocene Flora of Mugodzar and South Altai. Alma Ata, Kazakhstan, 123 pp., 32 plates.

RAYUSHKINA, G. S. (1982) *Fagus altaensis* Kornilova et Rayushkina. In: TAKHTAJAN, A. L. (ed.) Magnoliophyta Fossilia SSSR vol 2: 67-69. Leningrad, 216 pp., 172 plates.

RICHTER, R. (1948) Einführung in die zoologische Nomenklatur durch Erläuterung der Internationalen Regeln. 2nd ed. Senckenberg-Buch 15, Frankfurt, 252 pp.

RÖGL, F. (2001) Mid-Miocene Circum-Mediterranean paleogeography. In: LATAL, C., PILLER, W. E. (eds.) Environments and Ecosystem Dynamics of the Eurasian Neogene (EEDEN) Stratigraphy and Palaeogeography. Workshop Graz. Berichte des Institutes fuer Geologie und Paläontologie der Karl-Franzens-Universität Graz/Austria, Band 4, 60 pp.

SACHSE, M., MOHR, B. (1996) Eine obermiozäne Makro- und Mikroflora aus Südkreta (Griechenland), und deren paläoklimatische Interpretation. – Vorläufige Betrachtungen. N. Jb. Geol. Paläont. Abh. 200 (1/2): 149-182.

SAPORTA, G. (1867) Études sur la végétation du Sud-Est de la Provence a l'époque tertiaire. 3me partie. Ann. Sci. Nat. Bot. 5 (8): 5-136, 15 plates.

SAPORTA, G. (1884) Nouvelles observations sur la flore fossile de Mogi dans le Japon méridional. Paris, Libraire de l'académie de médecine: 1-36, 4 plates.

SCHMID, E. (2000) Palynologische Untersuchungen an Phosphoritknollen (Mitteloligozän) aus dem Tagebau Cospuden (Leipziger Bucht). M.Sc. Thesis, University of Vienna, 98 pp., 26 plates.

SHWAREVA, I. J. (1983) The Miocene flora of the Predkarpatye (in Russian). Acad. Sc. Ukrainian SSR, Kyiv, 160 pp., 80 plates.

SHEN, C.-F. (1992) A monograph of the genus *Fagus* Tourn. ex L. (Fagaceae). Ph.D. Dissertation, The City University of N.Y., 390 pp.

SORDELLI, F. (1896) Studi sulla vegetazione di Lombardia. Milano, 300 pp., 44 plates.

STANFORD, A. M. (1998) The biogeography and phylogeny of *Castanea, Fagus*, and *Juglans* based on matK and ITS sequence data. Ph.D. Dissertation, University of North Carolina at Chapel Hill, 261 pp.

STEFANOFF, B., JORDANOFF, D. (1935) Studies upon the Pliocene flora of the Plain of Sofia (Bulgaria). Bulg. Acad. Sc., Sofia, 150 pp., 24 plates.

SUZUKI, K. (1959) On the flora of the Upper Miocene Tennoji formation in in the Fukushima basin, Japan, and its paleoecological aspect (in Japanese with English abstract and systematic descriptions). Monogr. Assoc. Geol. Collab. Jap., 9.

SZAFER, W. (1961) Miocene flora from Stare Gliwice in Silesia. Instytut Geologiczny Prace 33: 1-205, 26 plates.

TANAI, T. (1974) Evolutionary trend of the genus *Fagus* around the northern Pacific Basin. Symposium on Origin and Phytogeography of Angiosperms, Birbal Sahni Inst. of Palaeobotany, Spec. Publ. 1: 62-83, 5 plates.

TANAI, T. (1976) The revision of the Pliocene Mogi flora, described by Nathorst (1883) and Florin (1920). J. Fac. Sci., Hokkaido Univ. Ser. 4, vol 17 (2): 277-346, 10 plates.

TANAI, T. (1995) Fagaceous leaves from the Paleogene of Hokkaido, Japan. Bull. Nat. Sci. Mus., Tokyo, Ser. C, 21 (3, 4): 71-101, 6 plates.

TANAI, T., SUZUKI, N. (1965) Late Tertiary floras from north-eastern Hokkaido, Japan. Spec. Paper, Palaeont. Soc. Japan 10: 1-117, 22 plates.

TRALAU, H. (1962) Die spättertiären *Fagus*-Arten Europas. Bot. Not. 115 (2): 147-176, 4 plates.

UNGER, F. (1847) Chloris protogaea. Leipzig, 150 pp., 50 plates.

VAN DER BURGH, J. (2001) Changes in the leaves of Fagaceae during the Late Miocene and Pliocene in the Lower Rhine embayment. Acta Palaeobot. 41 (2): 283-297, 2 plates.

VELITZELOS, E., KVAČEK, Z. (1999) Review of the Late Miocene flora of Vegora, western Macedonia, Greece. Acta Palaeobot. Suppl. 2: 419-427, 2 plates.

VIVIANI, D. (1833) Lettre de M. le Professeur Viviani à M. Pareto, sur les restes de plantes fossiles trouvés dans les gypses tertiaires de la Stradella, près Pavie. Mém. Soc. Géol. France 1 (7): 129-134, 3 plates.

WALTHER, H., ZASTAWNIAK, E. (1991) Fagaceae from Sośnica and Malczyce (near Wrocłav, Poland). A revision of original materials by Goeppert 1852 and 1855 and a study of new collections. Acta Palaeobot. 31 (1, 2): 153-199, 10 plates.

WALTHER, H., ZETTER, R. (1993) Zur Entwicklung der Paläogenen Fagaceae Mitteleuropas. Palaeontographica B 230: 183-194, 6 plates.

WEYLAND, H. (1934) Beiträge zur Kenntnis der rheinischen Tertiärfloren I. Floren aus den Kieseloolith- und Braunkohlenschichten der niederrheinischen Bucht. Abh. k. preuss. Geol. Landesanst., N. F., 161. Berlin, 122 pp., 22 plates.

WOLFE, J. A. (1966) Tertiary plants from the Cook Inlet region, Alaska. Geol. Survey Professional Paper 398-B: B1-B32, 8 plates.

WOROBIEC, G. (2000) Neogeńska flora liściowa z zagłebia wegla brunatnego w Bełchatowie. Ph.D. thesis, Inst. Bot. W. Szafera, Krakow.

ZASTAWNIAK, E. (1972) Pliocene leaf flora from Domański Wierch near Czarny Dunajec (Western Carpathians, Poland). Acta Palaeobot. 13 (1): 1-73, 30 plates.

YAKUBOVSKAYA, T. A. (1982) A new Miocene beech species from the European regions of the USSR. Paleont. Jour. 9 (4): 527-535 (English translation).

ZETTER, R. (1984) Morphologische Untersuchungen an *Fagus*-Blättern aus dem Neogen von Österreich. Beitr. Paläont. Österr. 11: 207-288, 15 plates.

ZHILIN, S. G. (1974) The Tertiary floras of the Plateau Ustjurt (Transcaspia) (in Russian). Komarov Botanical Institute of the Academy of Sciences of the USSR, Leningrad, 122 pp., 56 plates.

Figures on the next pages

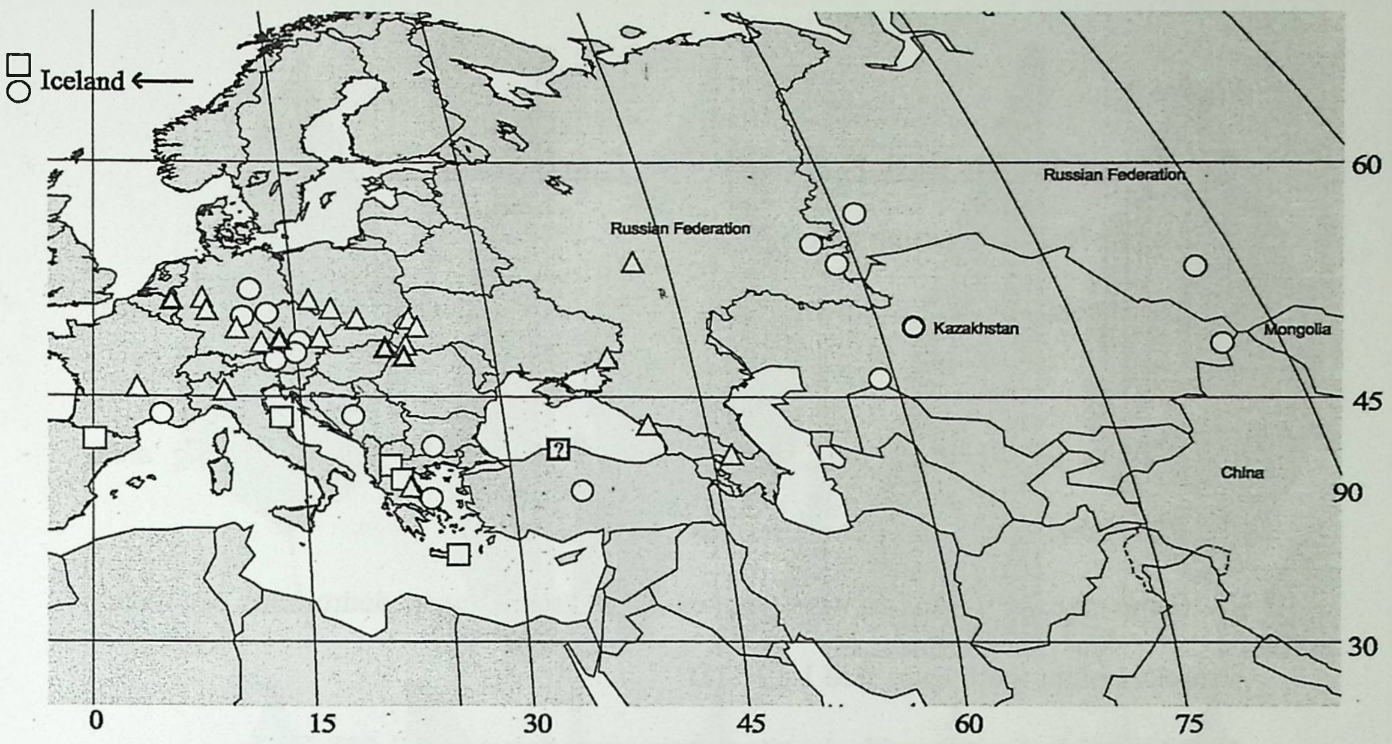


Figure 1 Origin and age of material included in the present study.
Note: Circles indicate occurrences of *F. castaneifolia* UNGER 1847, Late Oligocene to Karpatian (late Early Miocene). Squares - *F. gussonii* MASS. 1858, Late Miocene. Triangles - *F. haidingeri* KOV. 1856, Middle Miocene to Late Pliocene. Bold symbols indicate that material is based on figured specimens and descriptions. ? indicates that it is uncertain whether these specimens belong to *F. gussonii* or to *F. haidingeri*.

Figure 2 Paleogeographical map for the Aquitanian showing immigration pathways for *Fagus* to western Eurasia (map after RÖGL, 2001).
Note. Circles indicate Late Oligocene and Early Miocene occurrences of *F. castaneifolia* UNGER.

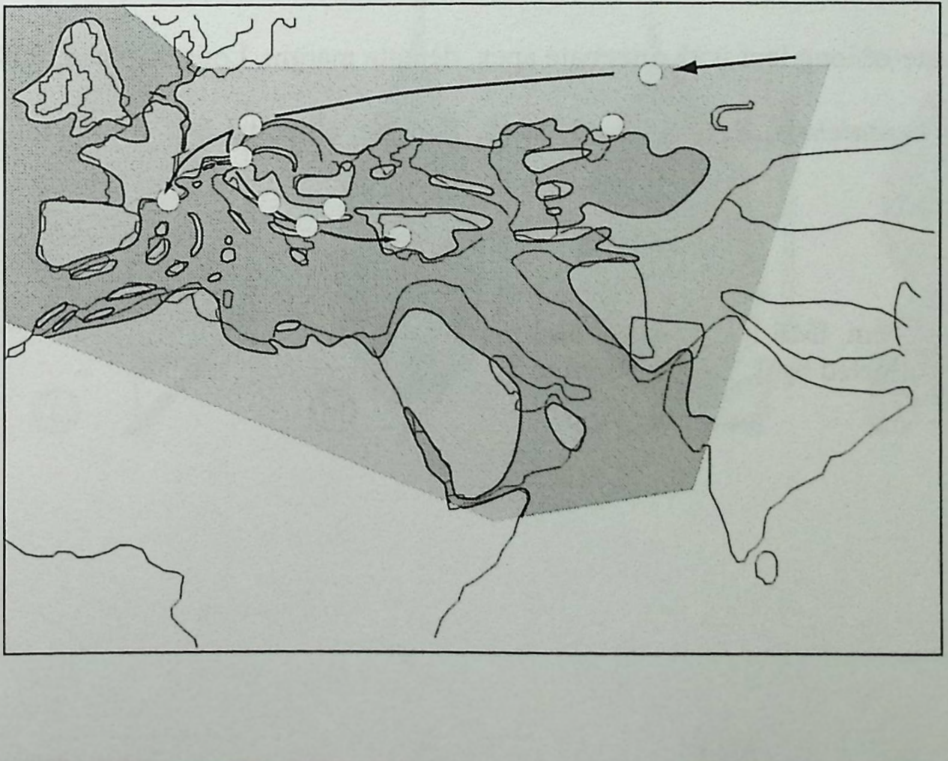


Figure 3

***Fagus longipetiolata* (incl. *F. brevipetiolata, F. tientaiensis*). China**

A. Trullate leaf of a fruiting twig, HIB 09778.

B. Same leaf, close-up showing craspedodromous secondary venation and leaf dentation.

C. Trullate leaf, fruiting twig, forest south of Longmenhe village, Ichang area, western Hubei, tree 1-114 TD.

D. Same tree, close-up showing convex IMR, (semi) craspedodromous secondary venation, blunt tooth apex, tree 1-121 TD.

E. Elliptical leaf with weakly dentate margin, same forest, tree 3-088 TD.

F, H. Elliptic leaves with pseudocraspedodromous secondary venation, entire margin, same forest, tree 2-126a, b TD.

G. Close-up of F showing pseudocraspedodromous venation.

I. Elliptic-oblong leaf, entire margin, Long Xi Shan, Nanping area, Fujian, 007 TD.

K. ***F. brevipetiolata*, K. M. Feng 13815 A Isotype**, trullate leaf.

L. Ovate (sun) leaf, Longmenhe, tree 3-090 TD.

M. Long-ovate leaf with attenuate apex, Long Xi Shan, 001a TD.

N. Ovate-oblong leaf with attenuate apex, dentate margin, Long Xi Shan, 008 TD.

O. ***F. tientaiensis*, S. S. Chen 3718 A, Isotype**, elliptical leaf with weakly dentate margin.

Scale = 5 cm. IMR = inter-secondary margin region.
TD = collected by T. Denk, stored in S.

FIGURE 3

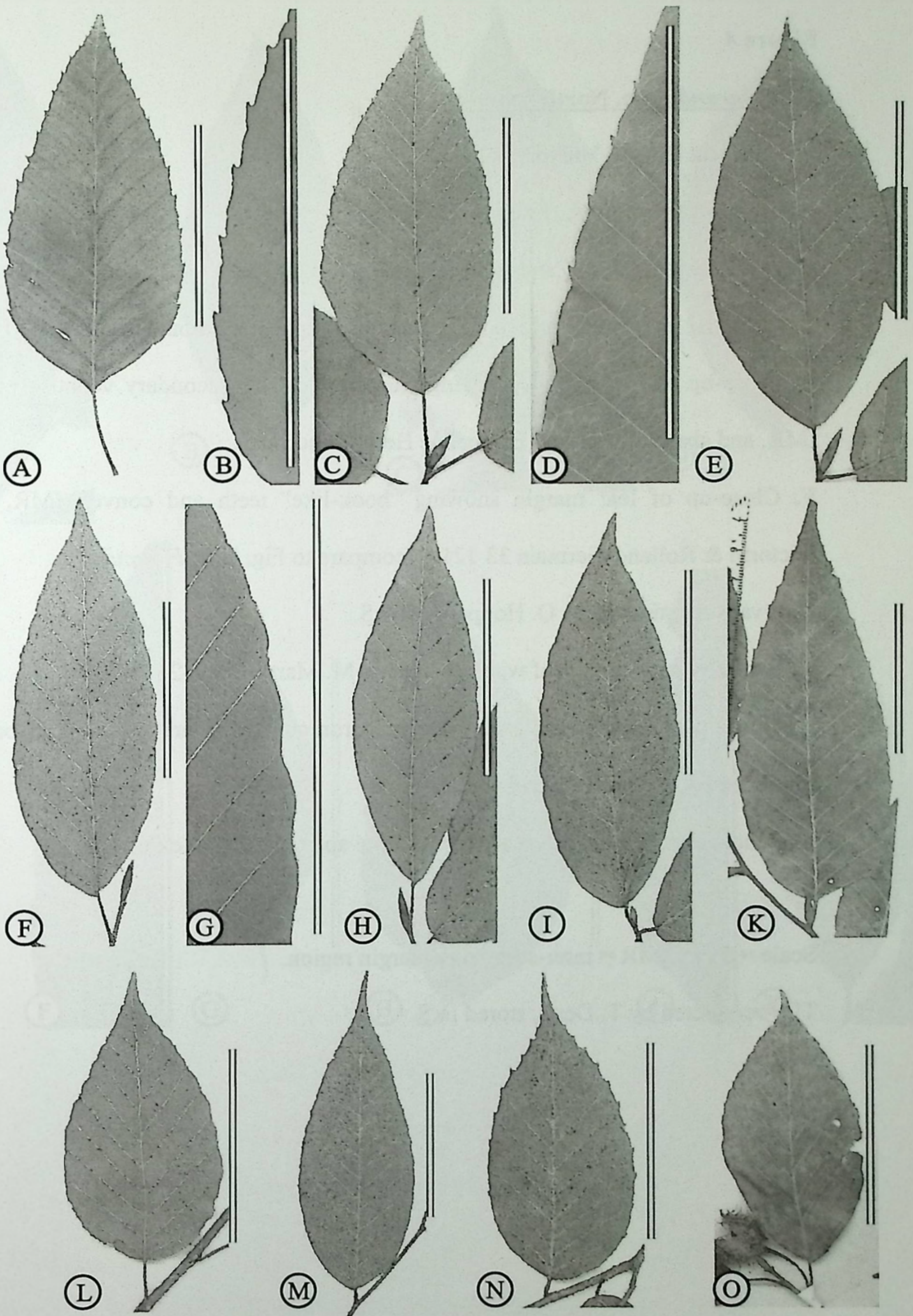


Figure 4

***Fagus grandifolia*. North America**

A. Elliptical leaf, A. Huelphers 1906 S.

B. Long ovate leaf, R. C. Friesner 10343a S.

C. Elliptical leaf, B. Rolland-Germain 26-7-1946 S.

D. Elliptical leaf with conspicuous dentation, Atlanta, Piedmont Park 5-1997 TD.

E. Close-up of leaf margin showing craspedodromous secondary venation, concave IMR, and sharp tooth apex, E. Koehne Herb. Dendrol. S.

F. Close-up of leaf margin showing "hook-like" teeth and convex IMR, Marie-Victorin & Rolland-Germain 33 121 S (compare to Fig. 7, E, *F. lucida*).

G. Ovate-elliptic leaf, P. O. Hopper 57067 S.

H. Broad ovate-elliptic leaf with blunt teeth, M. Martinez 1942 Mexico S.

I. Close-up of H showing pseudocraspedodromous secondary venation at base and semicraspedodromous towards the apex.

K. Lanceolate leaf with blunt teeth, attenuate apex, 152041 Mexico FSU.

Scale = 5 cm. IMR = inter-secondary margin region.

TD = collected by T. Denk, stored in S.

FIGURE 4

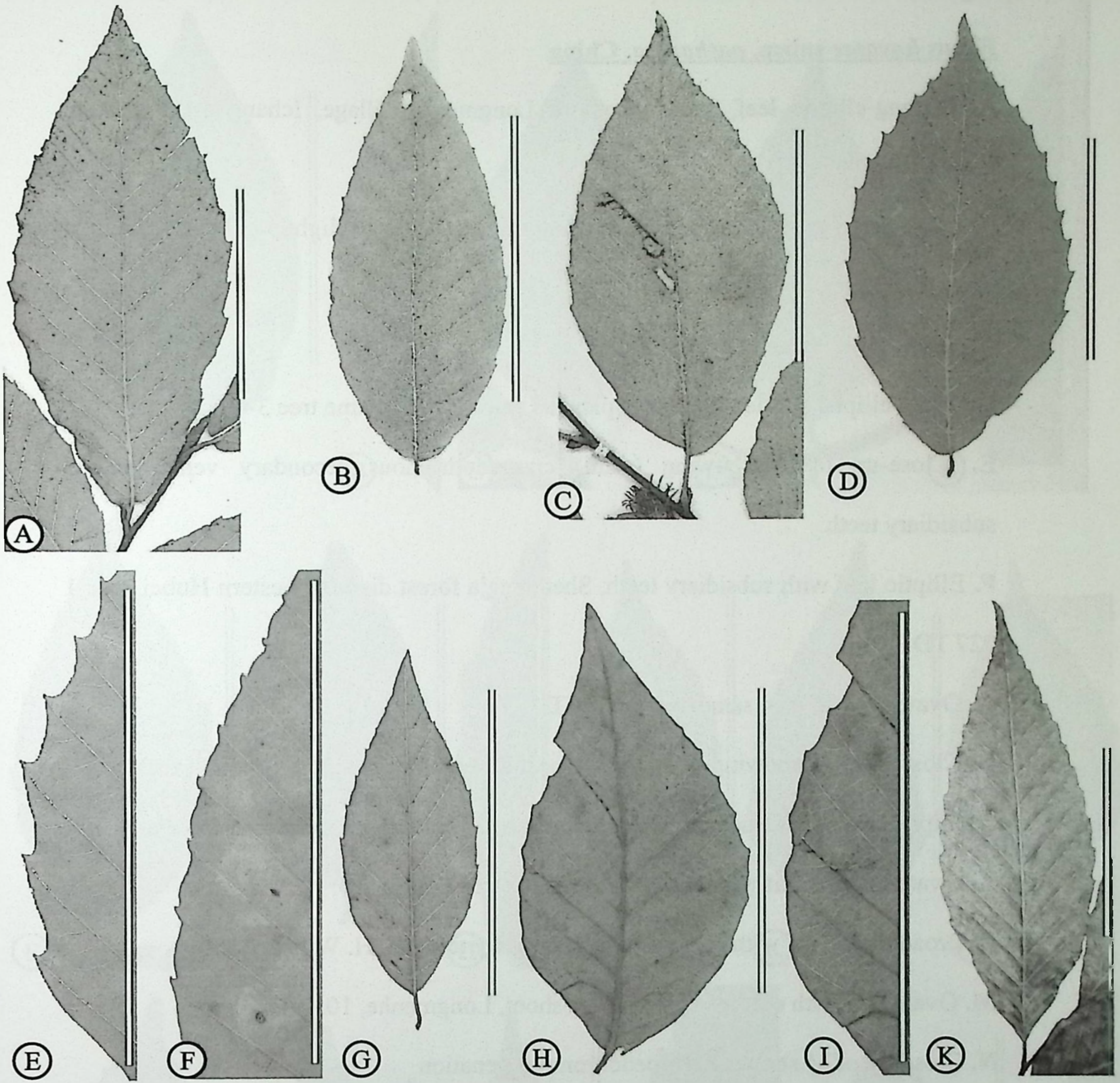


Figure 5

***Fagus hayatae* subsp. *pashanica*. China**

A. Oblong-elliptic leaf, forest south of Longmenhe village, Ichang area, western Hubei, tree 3 099 TD.

B. Close-up of A showing semicraspedodromous venation, slightly convex IMR, and blunt tooth apex.

C. Elliptic leaf, same tree 3-096 TD.

D. Ovate elliptic sun-leaf with conspicuous convex IMR, same tree 3-092 TD.

E. Close-up of D showing (semi) craspedodromous secondary venation and subsidiary teeth.

F. Elliptic leaf with subsidiary teeth, Shennongja forest district, western Hubei, tree 1 027 TD.

G. Ovate-elliptic leaf, same tree 1-029 TD.

H. Close-up of G showing (pseudo) craspedodromous venation and straight IMR.

I. Elliptic-ovate leaf, such shape often found in *F. haidingeri*, same tree 1-029a.

K. Ovate-trullate leaf with cordate base, same tree 1-027a TD.

L. Broad ovate leaf with cordate base, subsidiary teeth, E. H. Wilson 715b A.

M. Ovate leaf with cordate base, sucker-shoot, Longmenhe, 105 TD.

N. Close-up of M showing craspedodromous venation.

O. Narrow ovate-elliptic leaf of a seedling, Longmenhe, 103 TD.

P. Close-up of O showing hooked teeth and S-shaped IMR.

R. Aberrant leaf with irregularly spaced secondary veins, Shennongja, tree 1 026 TD.

S. Close-up of R showing craspedodromous venation and pointed teeth.

Scale = 5 cm in A, C, D, F, G, I-M, O, and R; 3 cm in B, H, N, and S; 1 cm in E, P. cm. IMR = inter-secondary margin region. TD = collected by T. Denk, stored in S.

FIGURE 5

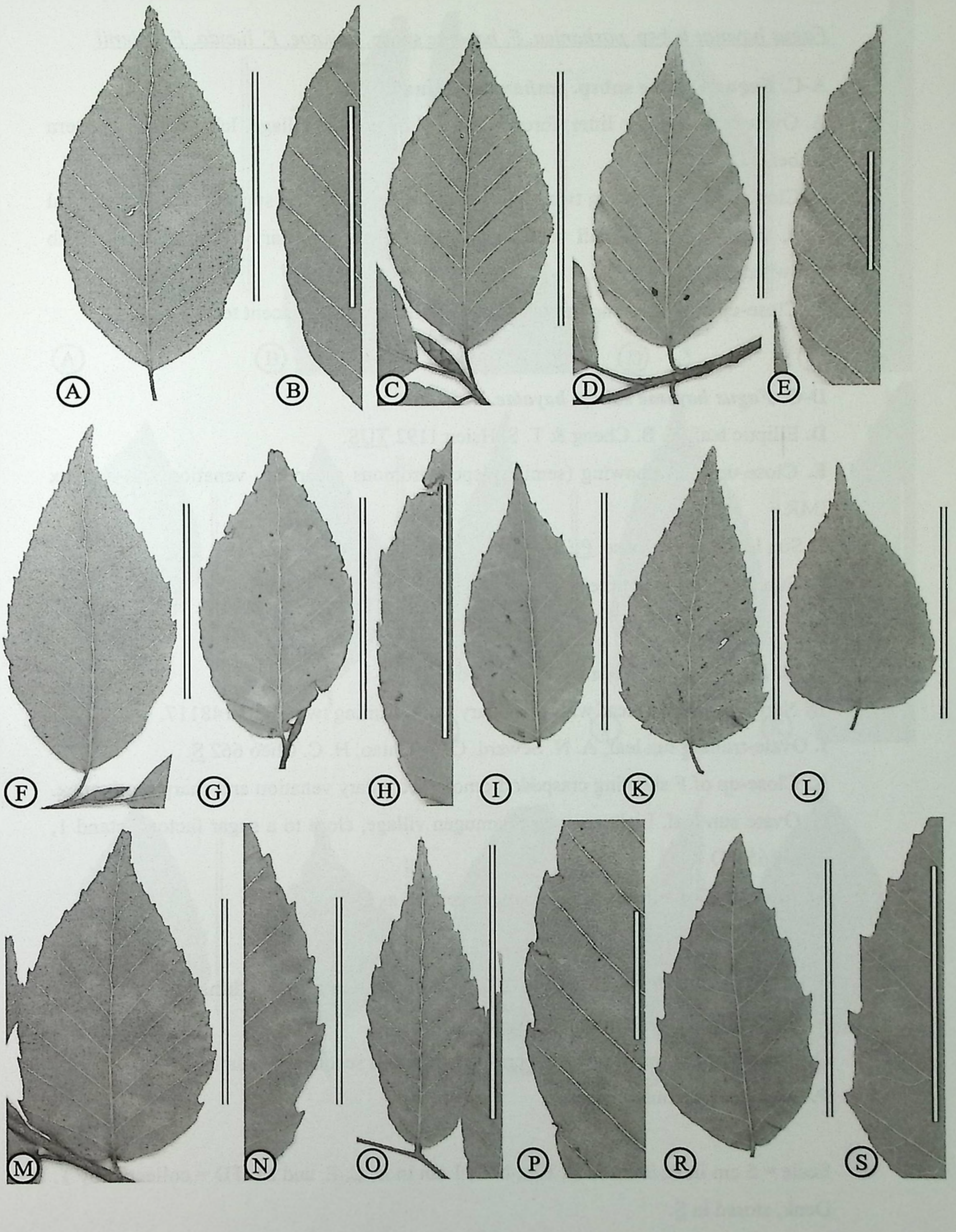


Figure 6

Fagus hayatae subsp. *pashanica*, *F. hayatae* subsp. *hayatae*, *F. lucida*, *F. chienii*

A-C. *Fagus hayatae* subsp. *pashanica*. China

A. Ovate leaf from the litter, forest south of Longmenhe village, Ichang area, western Hubei, TD.

B. Close-up of A showing two kinds of subsidiary teeth, one supplied by an abmedial vein, the other by a small veinlet originating from a tertiary vein (indicated with arrowhead).

C. Close-up of A showing irregular leaf margin between adjacent teeth.

D-G. *Fagus hayatae* subsp. *hayatae*. Taiwan

D. Elliptic leaf, Y. B. Cheng & T. S. Hsien 1192 TUS.

E. Close-up of A showing (semi) craspedodromous secondary venation and convex IMR.

F. Sun leaf, cuneate base, PE 1616641.

G. Sun leaf, same specimen.

H-M. *Fagus lucida*. China

H. Narrow ovate sun-leaf with subsidiary teeth, fruiting twig, HIB 148117.

I. Ovate-trullate sun leaf, A. N. Seward, C. Y. Chiao, H. C. Cheo 662 S.

K. Close-up of F showing craspedodromous secondary venation and sharp tooth apex.

L. Ovate sun-leaf, Lichuan area, Shamugen village, close to a sugar factory, stand 1, litter 165 TD.

M. Small leaf of a fruiting twig, same specimen as F.

N-P. *Fagus chienii*, W. C. Cheng 2903 A Isotype, sun leaves. China

N. Ovate elliptic leaf, entire margined.

O. Close-up of K showing pseudocraspedodromous secondary venation.

P. Ovate leaf, crenulate margin.

Scale = 5 cm in A; 3 cm in D, F-L, N-P; 1 cm in B, C, E, and M. TD = collected by T. Denk, stored in S.

FIGURE 6

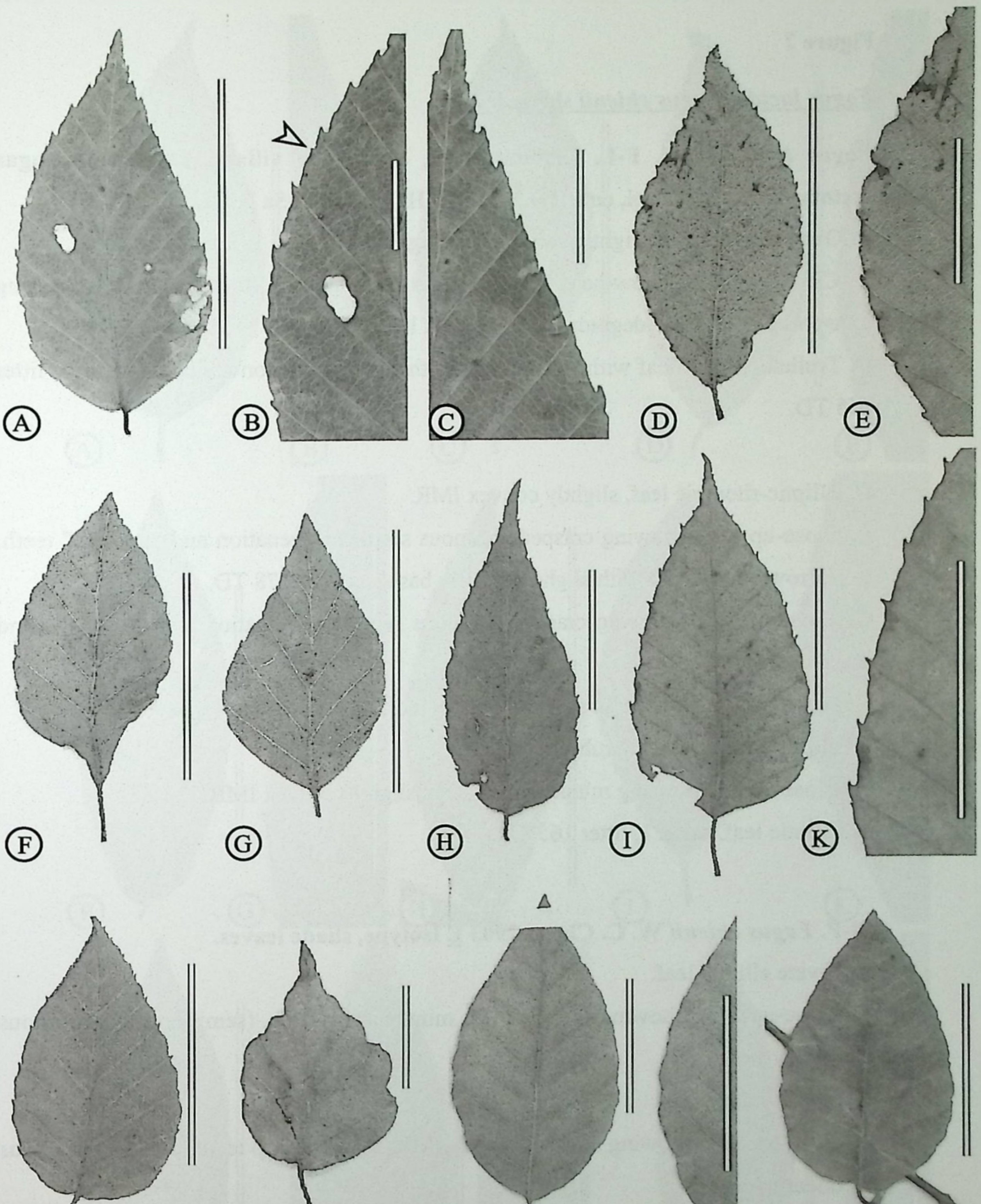


Figure 7

***Fagus lucida, Fagus chienii* shade leaves.**

***Fagus lucida*. A-C, F-L. Lichuan area, Shamugen village, close to a sugar factory, western Hubei, coll. TD. D, E: E. H. Wilson 715a K Lectotype.**

A. Ovate elliptic leaf, slightly convex to straight IMR, stand 1, litter 165 TD.

B. Close-up of A, arrow-head indicates loss of diagnostic (tooth) characters during transport and early biodegradation in the leaf litter.

C. Trullate-elliptic leaf with "cuspidate" teeth and slightly convex IMR, stand 1, litter 165 TD.

D. Elliptic-rhombic leaf, slightly convex IMR.

E. Close-up of D showing craspedodromous secondary venation and "hooked" teeth.

F. Narrow elliptic leaf with slightly cordate base, stand 1, 178 TD.

G. Close-up of F showing craspedodromous secondary venation, straight IMR, and sharp teeth.

H. Narrow elliptic leaf with straight IMR, stand 1, 179 TD.

I. Elliptic leaf, stand 1, shrub 182 TD.

K. Close-up of I showing minute sharp teeth, slightly convex IMR.

L. Elliptic leaf, stand 1, litter 165 TD.

M-P. *Fagus chienii* W. C. Cheng 2903 E Isotype, shade leaves.

M. Ovate elliptic leaf.

N. Close-up of M showing convex IMR, minute sharp teeth, (semi) craspedodromous secondary venation.

O. Ovate-oblong leaf.

P. Close-up of O showing slightly convex IMR, minute sharp teeth, craspedodromous secondary venation.

Scale = 5 cm in A, C, D, F, H, I, L, M, and O; 3 cm in B, E, G, K, N, and P.

IMR = inter-secondary margin region. TD = collected by T. Denk, stored in S.

FIGURE 7

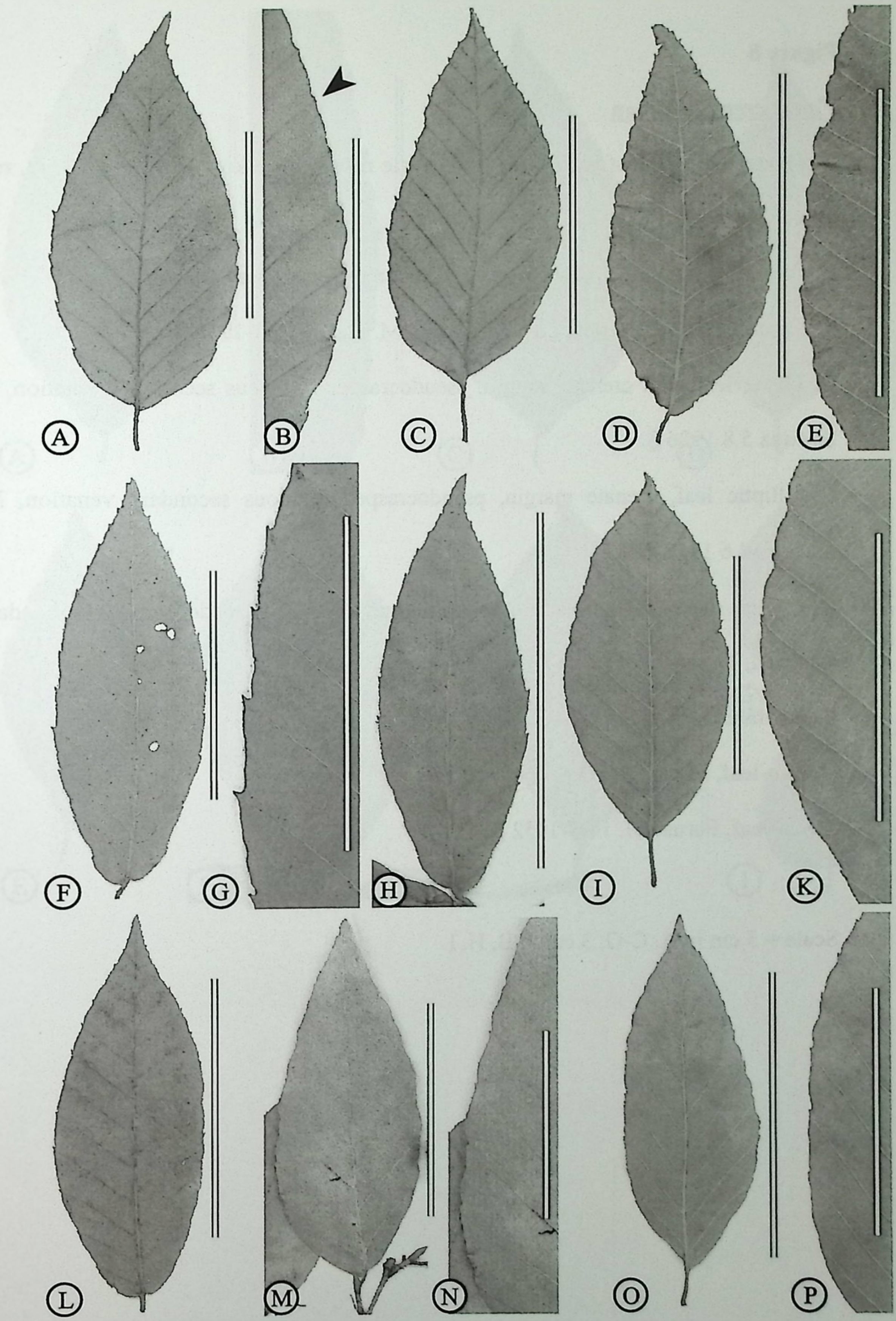


Figure 8

***Fagus crenata*. Japan**

A. Ovate-rhombic leaf with crenulate-dentate margin, Nietkow k Zielnoej Gory, rev. Shen K.-F. 1991 BIN.

B. Close-up of A showing (semi) craspedodromous secondary venation.

C. Ovate-rhombic leaf with crenate margin, M. Furuse 22 7 1958 S.

D. Ovate leaf with crenate margin, pseudocraspedodromous secondary venation, T. Sawada 5 8 1926 S.

E. Elliptic leaf, crenate margin, pseudocraspedodromous secondary venation, M. Furuse 14 6 1952 S.

F. Broad ovate-elliptic leaf, crenate margin, pseudocraspedodromous secondary venation, T. Satomi (1 8 1957) 15296 S.

G. Rhombic sun-leaf, Kirino S. 819 S.

H. Sun-leaf, Maxim. 1893 S.

I. Sun-leaf, Furuse M. 14-6-1952 S.

Scale = 5 cm in A, C-G; 3 cm in B, H, I.

FIGURE 8

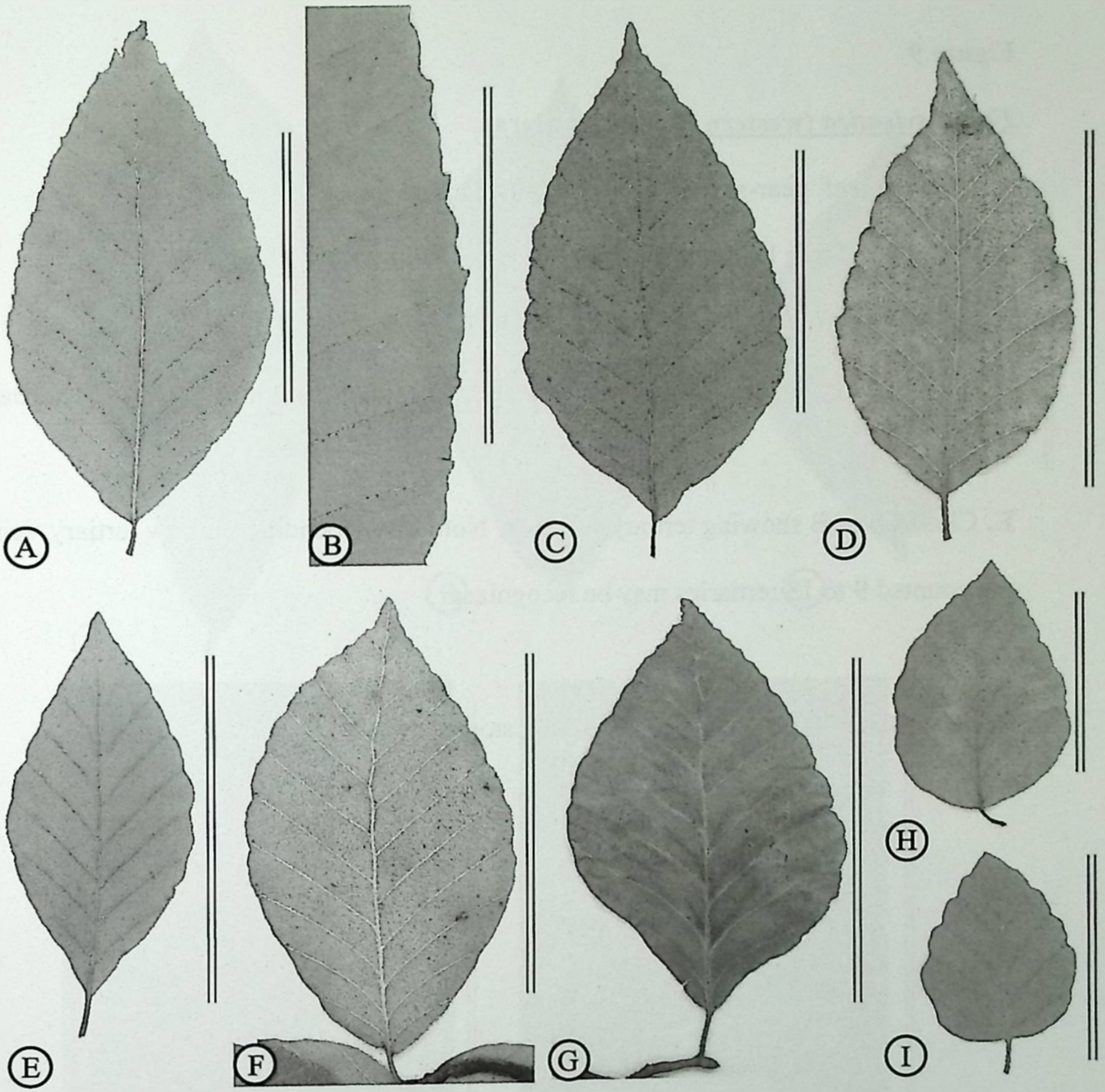


Figure 9

***Fagus sylvatica* (western Georgia, Adjara)**

A. Obovate leaf, pear-shaped base. 2000-09 Thikeri forest TD.

B. Obovate-elliptic leaf with pear-shaped base. 2000-09 Mt. Mtiralla TD.

C. Rhombic sun-leaf. 2000-09 Mt. Mtiralla TD.

D. Close-up of A showing tertiary venation. Note that there are only 4 (5) tertiary veins per cm.

E. Close-up of B showing tertiary venation. Note that depending on how tertiary veins are counted 9 to 13 tertiaries may be recognized.

Scale = 5 cm. TD = collected by T. Denk, stored in S.

FIGURE 9

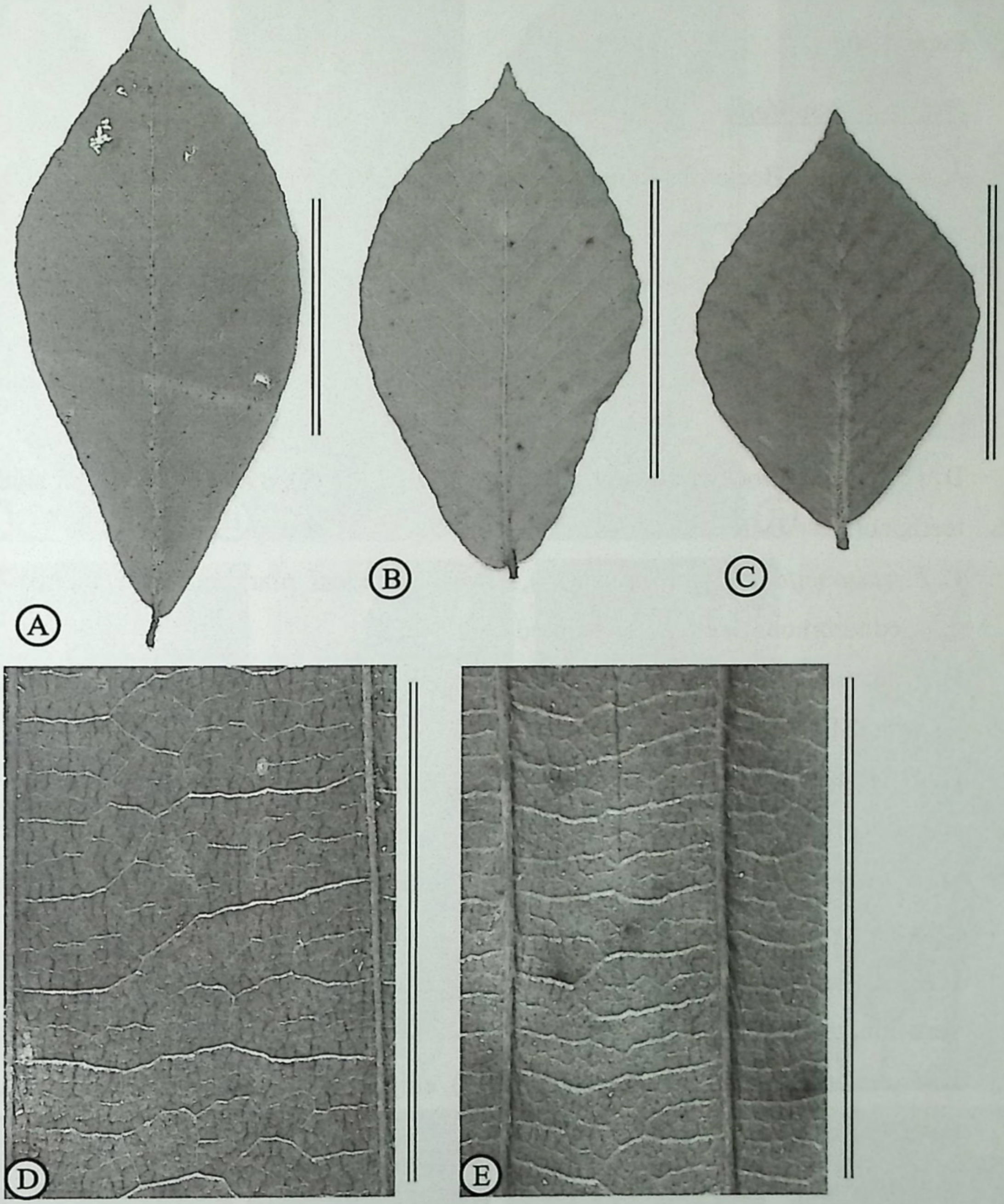


Figure 10

Fagus castaneifolia

A. *F. saxonica* Bockwitz-Borna, Germany BOB 2802 (2), ovate oblong leaf, straight IMR, no teeth preserved.

B. *F. pristina* Bois d'Asson, France 13059 (5), ovate elliptic leaf, no margin preserved.

C. *F. antipofii* Kumsuat, Kazakhstan 1016/108 (11), ovate elliptic leaf, no margin preserved.

D. *F. saxonica* Bockwitz-Borna, Germany BOB 2445 (2), ovate elliptic leaf, sharp teeth, concave IMR.

E. *F. castaneifolia* Kymi, Greece (1), narrow ovate leaf, margin dentate, (semi) craspedodromous, teeth not preserved.

F. *F. saxonica* Bockwitz-Borna, Germany BOB 2553 (2), ovate elliptic leaf, concave-straight IMR, "cuspidate" teeth.

G. *F. pristina* Manosque, France 13095 (5), narrow ovate elliptic leaf, dentate, craspedodromous secondary venation.

H. *F. castaneifolia* UNGER 1847 pl. 28 fig. 1, **Holotype** (8, 9), narrow elliptic leaf, concave IMR, sharp teeth.

I. *F. castaneifolia* Kymi, Greece (1), elliptic leaf, craspedodromous secondary venation, teeth not preserved.

K. *F. castaneifolia* Ognanovo, Bulgaria (1), elliptic leaf, straicht IMR, minute sharp teeth, craspedodromous secondary venation.

L. *F. pristina* Manosque, France 13095 (5), elliptic leaf, no margin preserved.

M. *F. antipofii* Kumsuat, Kazakhstan 1016/109a (11), narrow elliptic leaf, poorly preserved leaf margin, secondary venation pseudocraspedodromous (basal), to craspedodromous, minute sharp teeth (apical).

Scale = 5 cm. IMR = inter-secondary margin region.

FIGURE 10

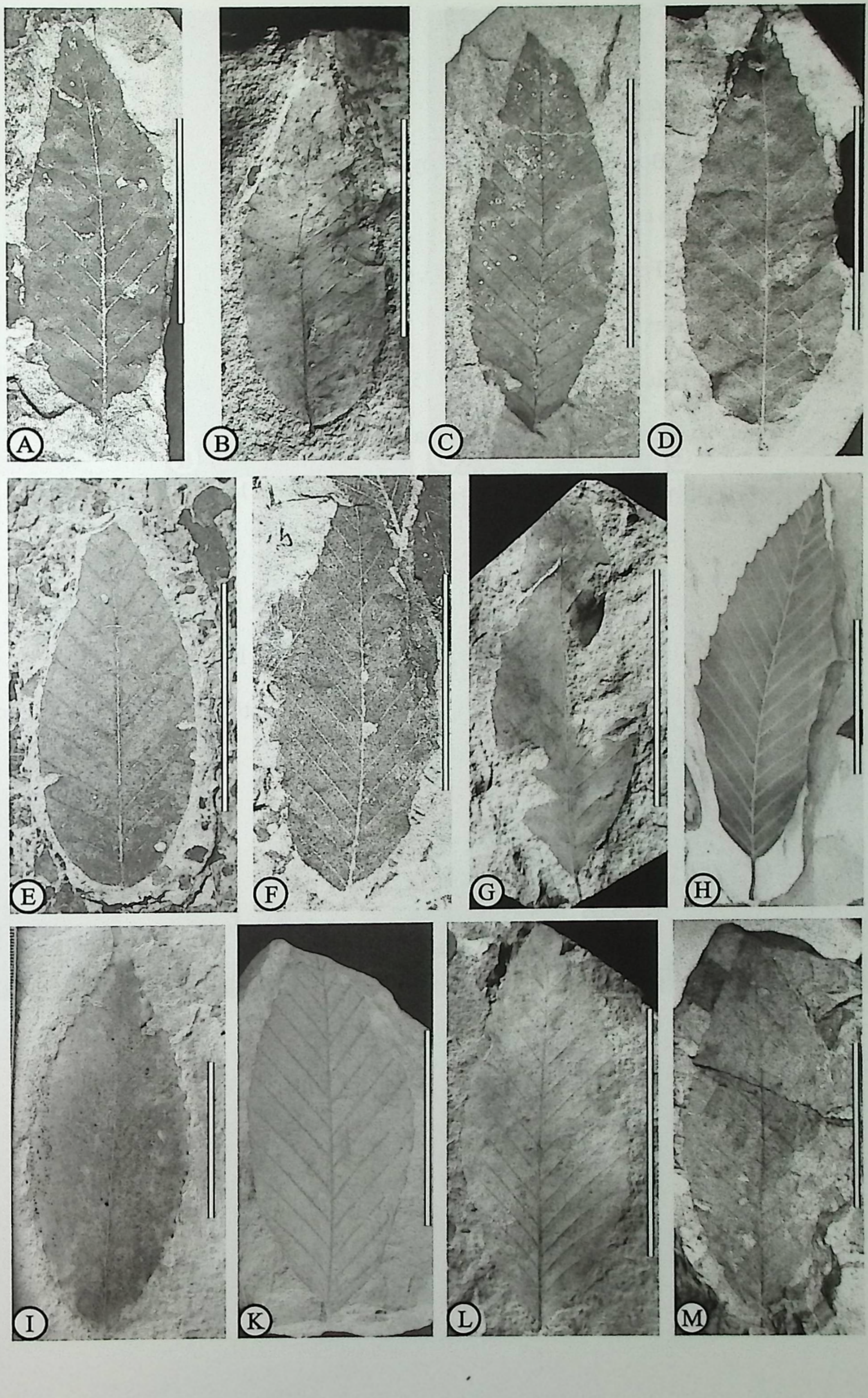


Figure 11

Fagus castaneifolia

A. *F. saxonica* Bockwitz-Borna, Germany BOB 2519 (2), ovate leaf with cuspidate teeth, straight to concave IMR.

B. *F. attenuata* Fohnsdorf, Austria (7, 8), ovate elliptic leaf with cuspidate teeth, straight to convex IMR.

C. *F. pristina* Manosque, France 13057 (5), ovate elliptic leaf, badly preserved margin, craspedodromous secondary venation.

D. *F. antipofii* Kumsuat, Kazakhstan 1016/78 (11), elliptic leaf, badly preserved margin.

E. *F. pristina* Bois d'Asson, France 13069 (5), elliptic leaf, no margin preserved.

F. *F. pristina* Bois d'Asson, France 12710 (5), broad ovate leaf, no margin preserved.

G. *F. antipofii* Kumsuat, Kazakhstan 1016/106, broad elliptic leaf, cordate base, badly preserved margin.

Scale = 5 cm. IMR = inter-secondary margin region.

FIGURE 11

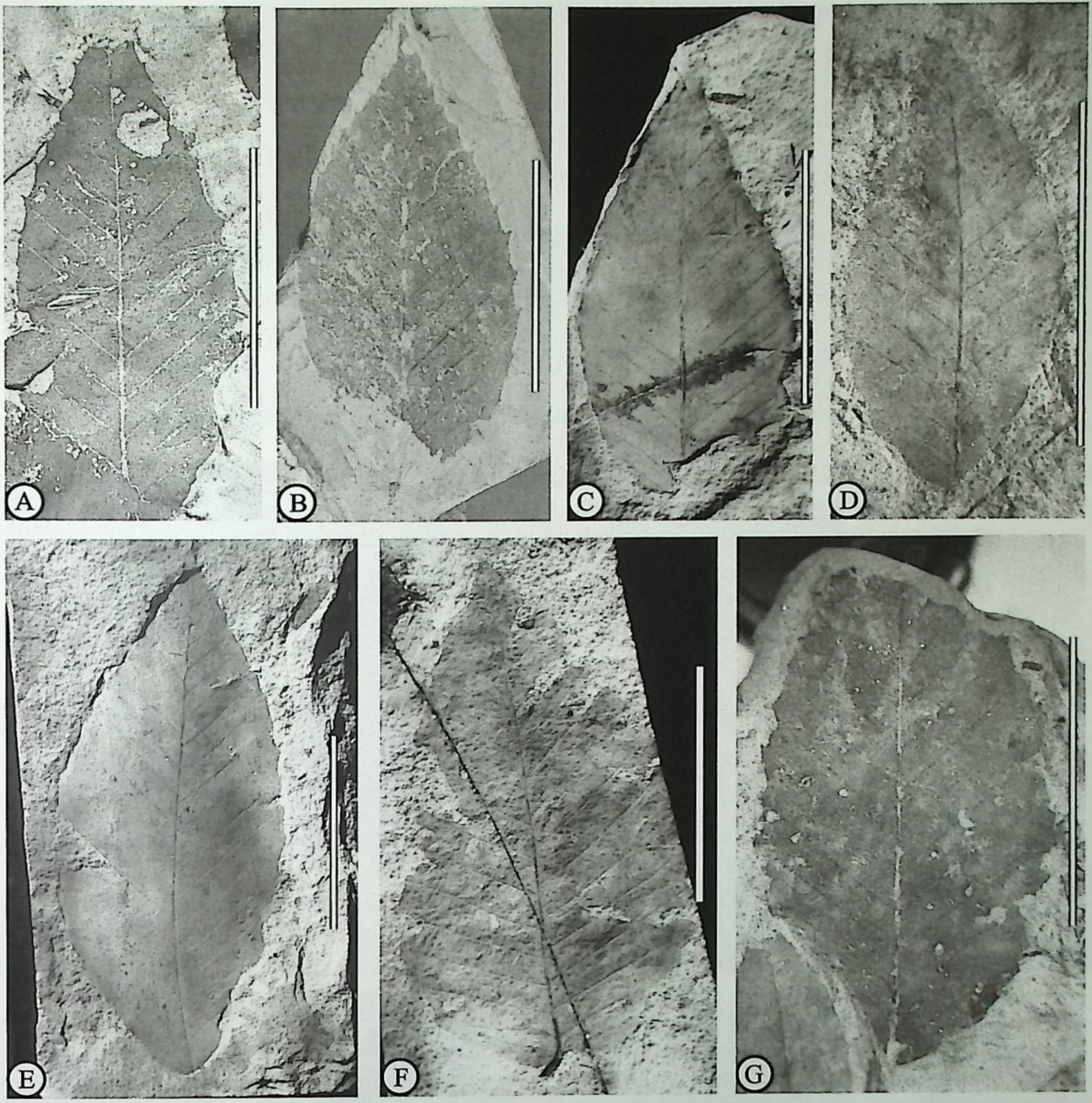


Figure 12

Fagus deucalionis*, *Fagus gussonii

A. *F. deucalionis*, cupule (1), Vegora, Greece.

B-M. *F. gussonii*. **B-F, I, K** Vegora (1). **G, H** Ellasona, Greece (1).

B. Elliptic leaf with crenulate margin, pseudocraspedodromous secondary venation, "*F. sylvatica*" type.

C. Obovate leaf with pear-shaped base, very similar to *F. sylvatica* from the northern and eastern Black Sea coast (compare to Fig. 9, A).

D. Elliptic leaf, pseudo/semicraspedodromous secondary venation, crenulate.

E. Ovate- trullate leaf, dentate, convex IMR, "*F. longipetiolata*" type, S115964; compare to Fig. 3, A-C.

F. Elliptic leaf, dentate, convex IMR, S115995.

G, H. Ovate trullate leaf, margin badly preserved, pseudo/semicraspedodromous, "*F. longipetiolata*" type.

I. Broad ovate leaf, weakly dentate, pseudo/semicraspedodromous secondary venation.

K. Broad elliptic leaf, weakly dentate, S116036.

L. Makrilia, Crete (1), elliptic leaf, very similar to *F. sylvatica* (compare Fig. 9, B, C).

M. *F. marsilii* Massalongo & Scarabelli 1859 pl. 9, fig. 19, Senigallia, Italy; elliptic leaf, very similar to *F. sylvatica* (compare Fig. 9, B, C).

Scale = 5 cm, 1 cm in A.

IMR = inter-secondary margin region.

FIGURE 12

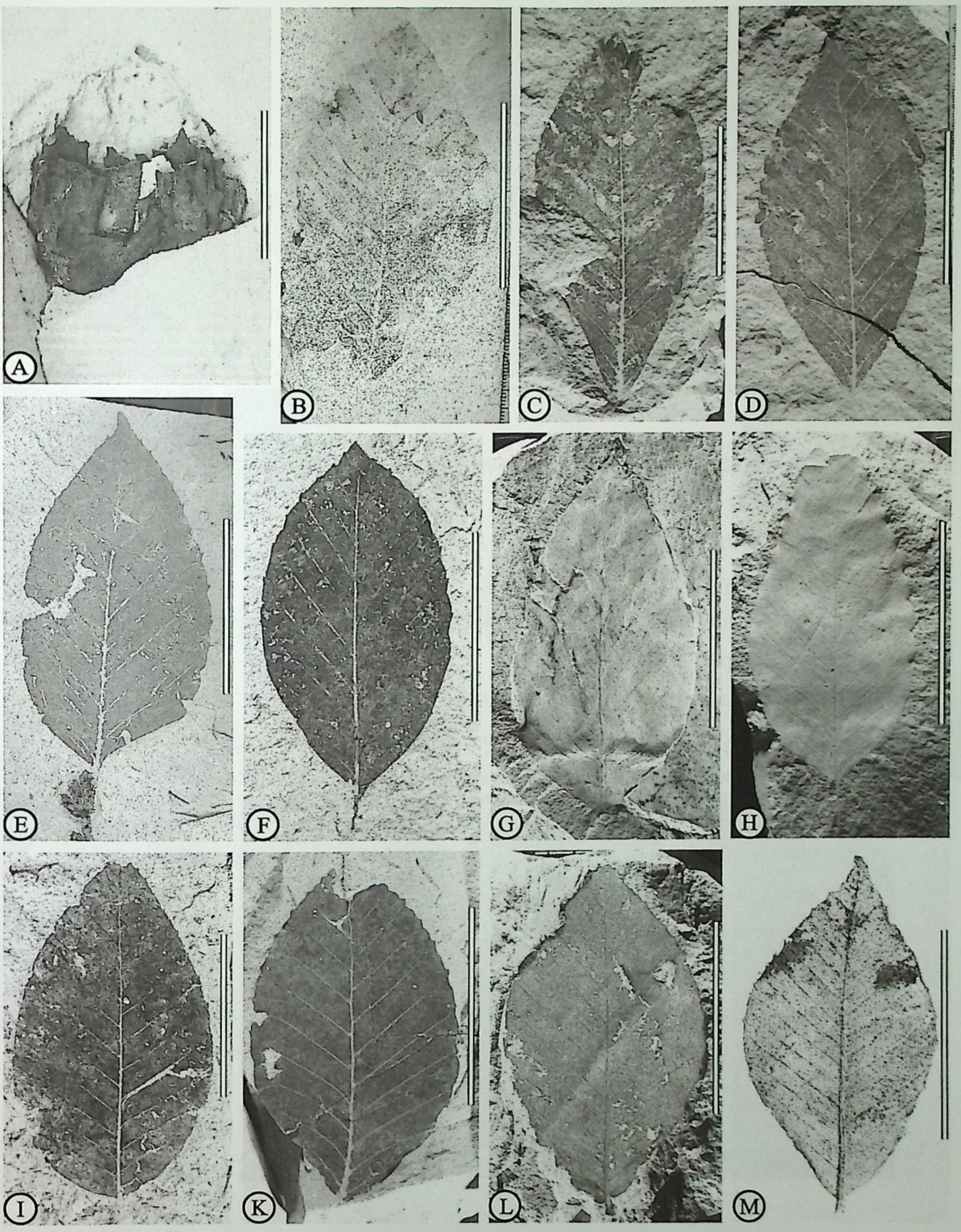


Figure 13

Fagus haidingeri

A-D *"sylvatica"- "crenata"* types.

A. *F. kraeuselii, F. pliocenica* subsp. *willershausensis* Willershausen, Germany 39214 (4), elliptic leaf.

B. *F. kraeuselii* Frankfurt, Germany KN35 (3), ovate leaf, crenate margin, (brochidodromous) pseudocraspedodromous secondary venation.

C. *F. orientalis* var. *fossilis* Krynka, Northern Caucasus 173a (11), elliptic leaf.

D. *F. attenuata* Kortumova Hora, Ukraine 671 (10).

E. *F. kraeuselii, F. pliocenica* subsp. *willershausensis* Willershausen, Germany P3810, 8335 (4), ovate-elliptic leaf.

F. *F. kraeuselii, F. pliocenica* subsp. *willershausensis* Willershausen, Germany 101 86 (4), weakly dentate, elliptic leaf.

G. *F. kraeuselii* Frankfurt, Germany KN4 (3), elliptic leaf, convex IMR, blunt teeth, *"hayatae"* type.

H. *F. silesiaca* **Isotype** (2), Sośnica, Poland (ovate) elliptic leaf, semicraspedodromous secondary venation, straight to slightly convex IMR, blunt teeth, very similar to *F. hayatae* subsp. *pashanica* (compare Fig. 5, A-L).

I. *F. pliocaenica* Niac, France 12449 (5), ovate elliptic leaf, poorly preserved margin.

K. *F. kraeuselii, F. pliocenica* subsp. *willershausensis* Willershausen, Germany 38149 (4), poorly preserved margin.

L. *F. attenuata* Mychyn, Ukraine 9/11 (11), ovate elliptic leaf with poorly preserved margin.

M. *F. orientalis fossilis* Armavir, Northern Caucasus 347/68 (11), ovate elliptic leaf.

Scale = 5 cm, 2.5 cm in M.

IMR = inter-secondary margin region.

FIGURE 13

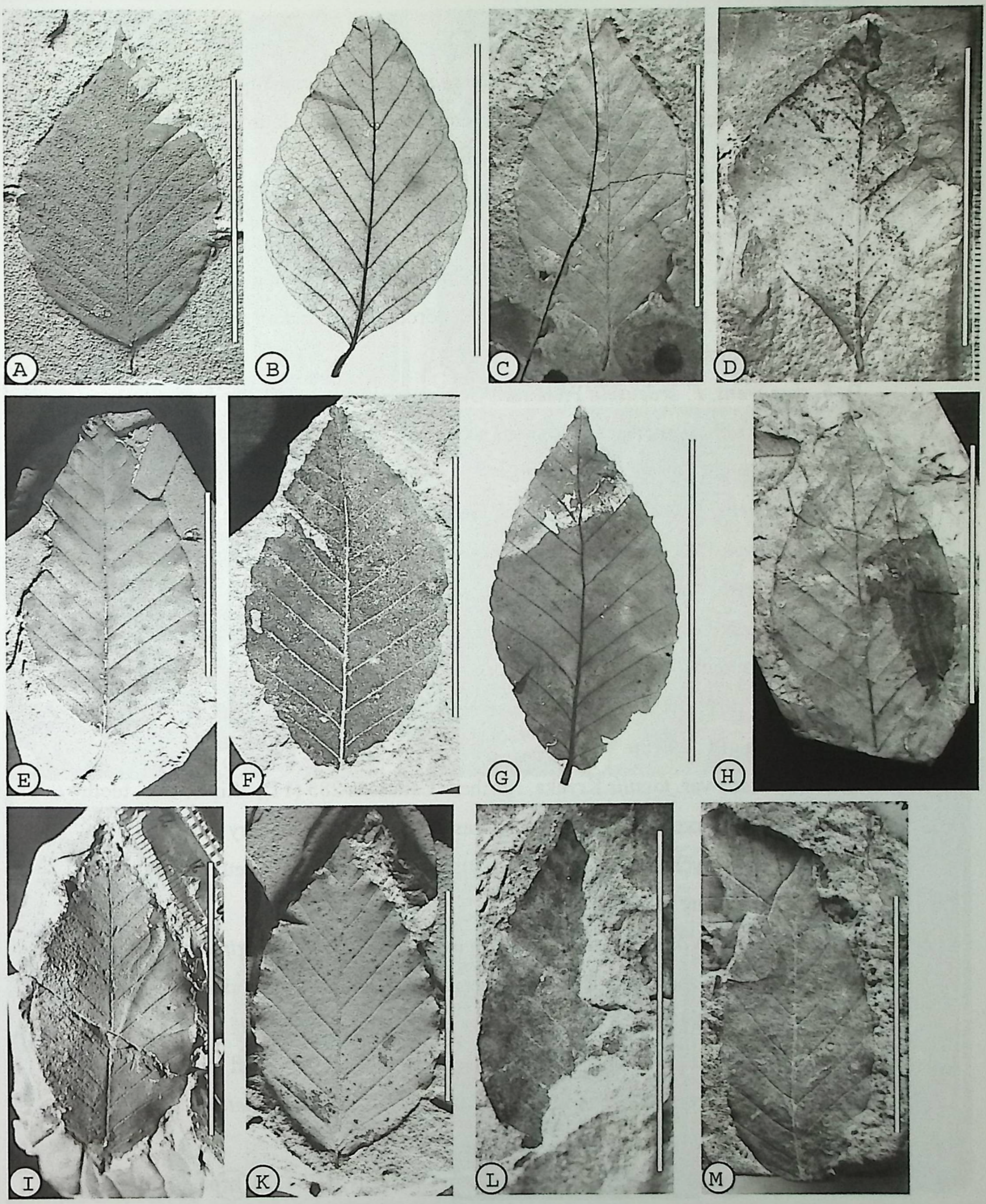


Figure 14

Fagus haidingeri

A. *F. kraeuselii, F. pliocenica* subsp. *willershausensis* Willershausen, Germany 16 689a (4), ovate elliptic leaf, minute sharp teeth, (semi) craspedodromous secondary venation.

B. *F. orientalis* var. *fossilis* Krynka, Northern Caucasus 458 (11), long elliptic leaf, no margin preserved.

C. *F. kraeuselii, F. pliocenica* subsp. *willershausensis* Willershausen, Germany 5733 (4), elliptic leaf, minute teeth, (semi) craspedodromous secondary venation, similar to *F. chienii* (compare Fig. 7, O).

D. *F. decurrens, F. kraeuselii* Frankfurt, Germany KN 24 (3), elliptic leaf, convex IMR, blunt teeth, semicraspedodromous secondary venation, *"hayatae* subsp. *pashanica"* type.

E. *F. decurrens, F. kraeuselii* Frankfurt, Germany KN 09 (3), elliptic oblong leaf, slightly convex IMR, semicraspedodromous secondary venation, sharp teeth, subsidiary teeth, *"hayatae* subsp. *pashanica"* type.

F. *F. orientalis fossilis* Armavir, Northern Caucasus 347a/69 (11), long ovate leaf, no margin preserved.

G. *F. attenuata* Kortumova Hora, Ukraine 699 (10), ovate elliptic leaf, similar to shade leaves of *F. chienii.*

H. *F. orientalis* var. *fossilis* Krynka, Northern Caucasus 285 (11), elliptic leaf, teeth not entirely preserved and/or blunt, semicraspedodromous secondary venation.

I. *F. attenuata* Mychyn, Ukraine 13/55 (10), (ovate) elliptic leaf, teeth incompletely preserved (compare to Fig. 7, B).

K. *F. haidingeri* Vösendorf, Austria (7, 8), ovate elliptic leaf, *"longipetiolata"* type.

L. Close-up of K showing convex IMR, semicraspedoromous secondary venation and "*longipetiolata*-like" teeth.

M. *F. decurrens, F. kraeuselii* Frankfurt, Germany KN 70 (3), broad ovate leaf, (semi) craspedodromous secondary venation, convex IMR, "*longipetiolata*-like" teeth.

N. *F. orientalis* var. *fossilis* Krynka, Northern Caucasus 1076 (11), broad elliptic leaf, no margin preserved.

O. *F. attenuata* Kosiv, Ukraine 14 (10), broad ovate leaf.

Scale = 5 cm, 2.5 cm in H, L. - IMR = inter-secondary margin region.

FIGURE 14

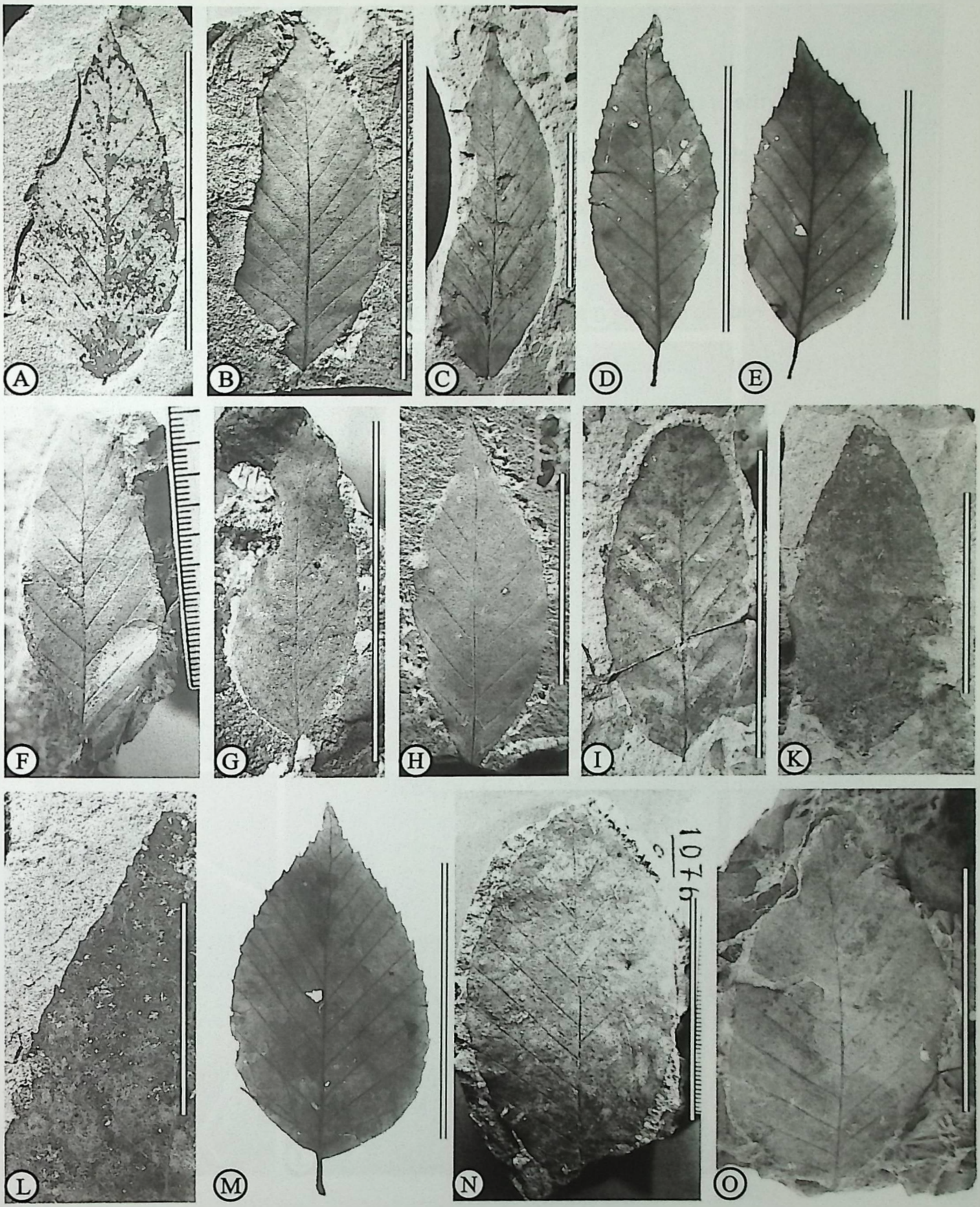


Figure 15

***Fagus* northern Italy (6)**

A-L. *Fagus* cf. *haidingeri*. Messinian

A. Ovate (sun-) leaf, Castagnito1 0013.

B. Elliptic-rhombic leaf, Castagnito 0050.

C. Elliptic leaf, no margin preserved, Scaparoni 0092.

D. Elliptic leaf, Scaparoni 0090.

E-I. Large elliptic leaves, no margin preserved.

E. Castagnito 2 0041.

F. Castagnito2 0040.

G. Scaparoni 0142.

H. Scaparoni 0131.

I. Scaparoni 0599.

K. Broad elliptic leaf, Scaparoni 0149.

L. Fragment of a large elliptic leaf, Scaparoni 0102.

M, N. *Fagus haidingeri*

M. Ovate elliptic leaf, Valmanera, Piedmont, Pliocene no. 29.

N. Small, elliptic (sun-) leaf, Valmanera, Piedmont, Pliocene no. 27.

Scale = 5 cm.

FIGURE 15

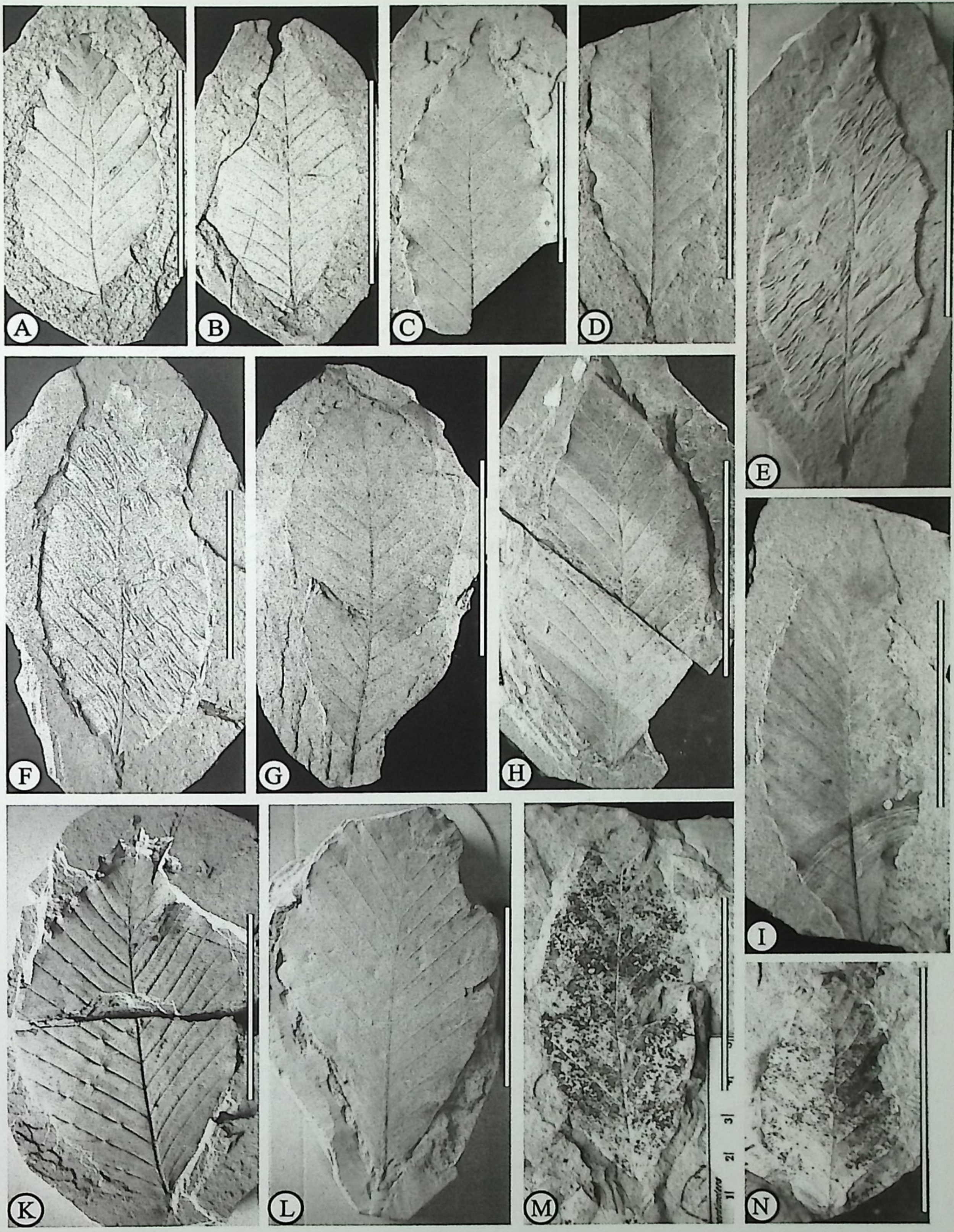
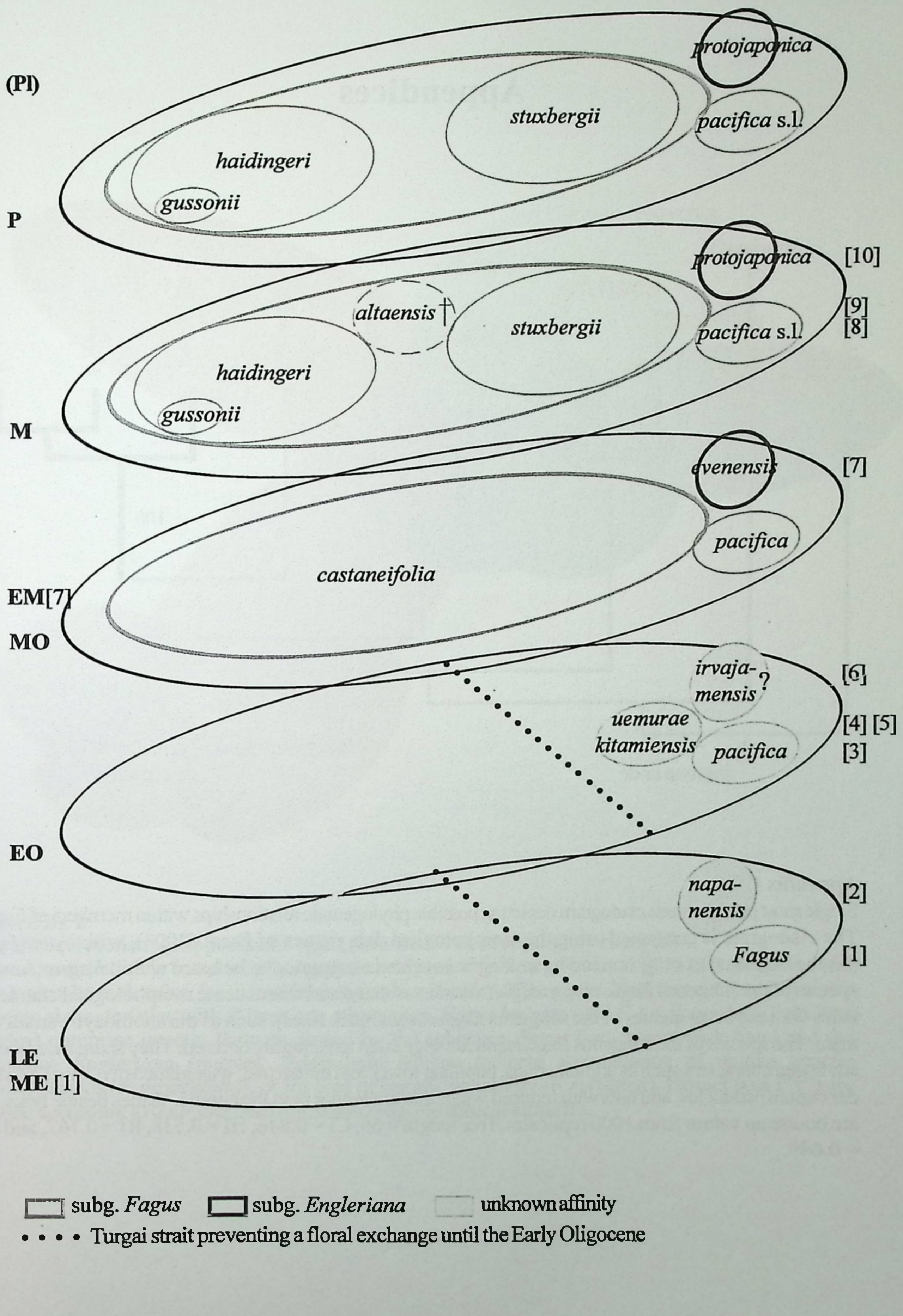


Figure 16

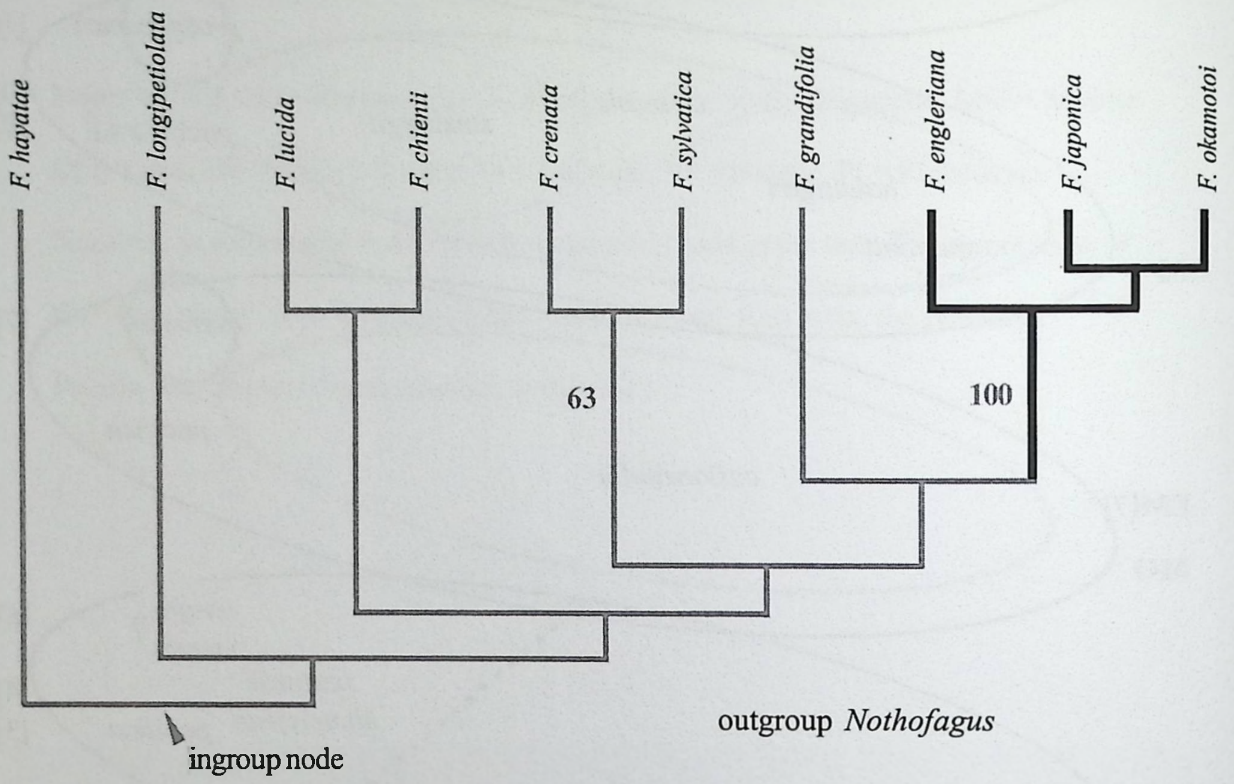
Diagram showing putative diversification within *Fagus* from the Eocene to present.

Note. ME = Middle Eocene, LE = Late Eocene, EO = Early Oligocene, MO = Middle Oligocene, EM = Early Miocene, M = Miocene, P = Pliocene, Pl = Pleistocene. Numbers in rectangular brackets refer to numbers used in the text. The orientation of the “time slices” is so that Europe lies in the west, and East Asia, the Northern Pacific, and western North America in the east.

FIGURE 16

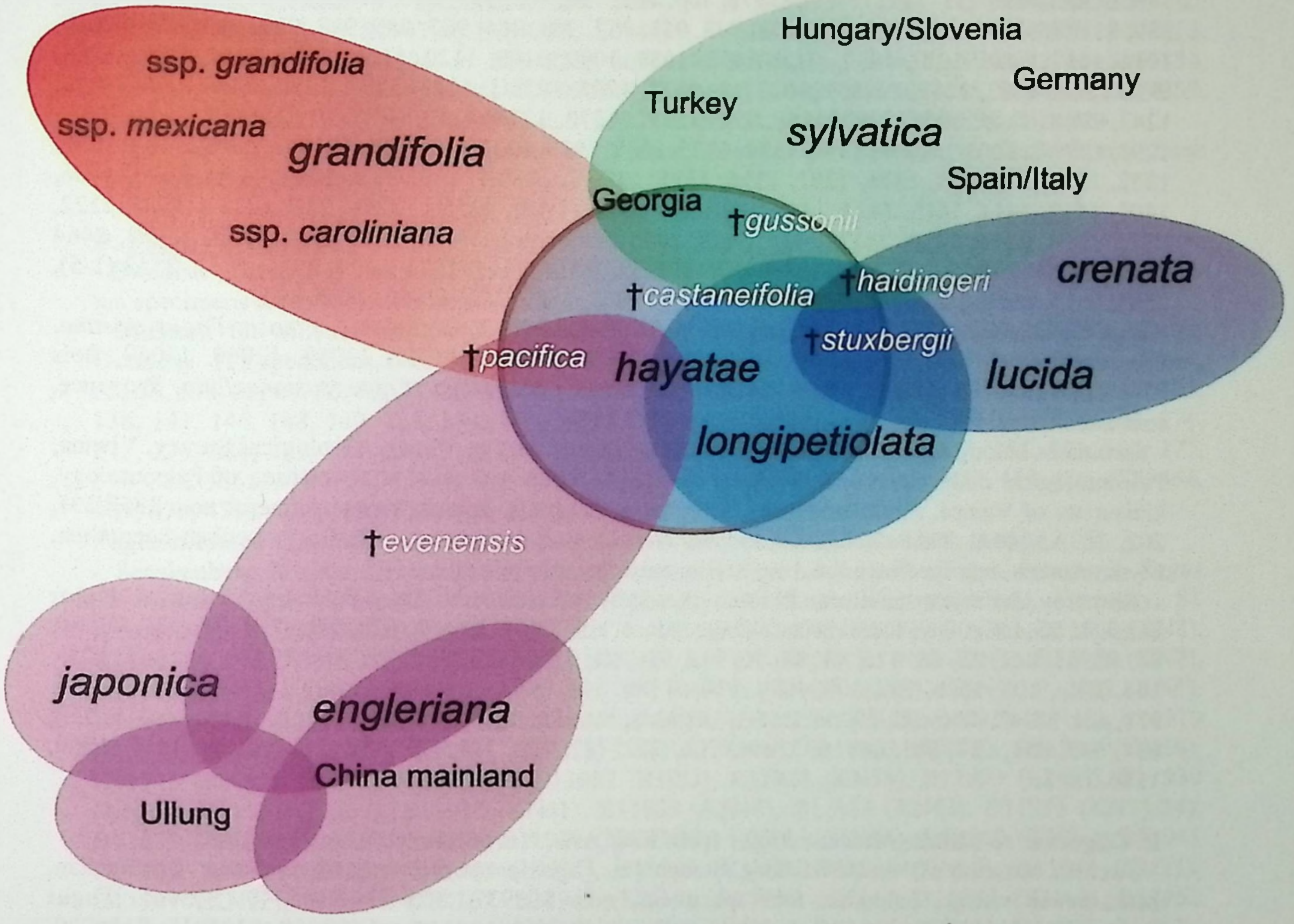

(Pl)
protojaponica
stuxbergii
pacifica s.l.
haidingeri
gussonii
P
protojaponica
[10]
altaensis †
stuxbergii
[9]
pacifica s.l.
[8]
haidingeri
gussonii
M
evenensis
[7]
pacifica
castaneifolia
EM[7]
MO
irvaja-mensis ?
[6]
uemurae kitamiensis
[4] [5]
pacifica
[3]
EO
napa-nensis
[2]
Fagus
[1]
LE
ME [1]
subg. Fagus
subg. Engleriana
unknown affinity
• • • • Turgai strait preventing a floral exchange until the Early Oligocene

Appendices



Appendix 1

Single most parsimonious cladogram depicting possible phylogenetic relationships within members of *Fagus*. The cladogram is generated using the morphological data matrix of Denk (2003), with *Nothofagus* (Nothofagaceae) as outgroup to *Fagus*. *Fagus hayatae* is suggested to be basal within *Fagus*. Among species of the subgenus *Fagus*, *F. grandifolia* is most isolated and shares some morphological characteristics with the three species of the subgenus *Engleriana* (black lines), such as the anomocytic small stomata. The species of the subgenus *Engleriana* are suggested to be highly derived. They share a number of advanced characters such as stipitate buds, papillate lower leaf epidermis, wax glaucosity, long and slender cupule peduncles, and nuts with reduced wings that are longer than the cupule. Values beside branches are bootstrap values from 1000 replicates.Tree length = 65, CI = 0.846, HI = 0.538, RI = 0.767, and RC = 0.649.



Appendix 2
Ancient and modern gene pools of *Fagus* (from GRIMM, 2003; slightly changed).
The reconstruction is based on phylogenetic analyses of nuclear ribosomal DNA ITS sequences and integrates the molecular, fossil, and biogeographical history of the genus. Note that every taxon shares genetic characteristics with at least one other taxon. *Fagus hayatae* (and *F. longipetiolata*, light blue circles) comprise genetic features shared by the subgenus *Fagus* (red, green, dark blue) and the subgenus *Engleriana* (purple). Bright/light colours indicate accumulation of unique genetic characteristics (*F. grandifolia*), or the loss of genetic variability (*F. sylvatica*). Extinct taxa ("†") are placed according to their morphological and biogeographical affinities.

Appendix 3: Fossil material studied

A. *Fagus castaneifolia*, Upper Oligocene to Lower (Middle) Miocene.

- Swedish Museum of Natural History, Stockholm. Kymi, Evia, Greece, three unnumbered specimens. Ognanovo, Rhodope Mts., Bulgaria, one unnumbered specimen.
- Museum für Mineralogie und Geologie, Dresden, Germany. *Fagus saxonica*. Bockwitz-Borna, Germany, around 250 specimens (many of the hand-specimens contain more than one leaf), BOB nos. 5a, 9b, 11a, 44/1, 46/4, 49/1, 91, 98/2, 109, 129a, 133/2, 135, 137/5 b, f, k, 193, 195, 200, 228, 282, 295/2 b, c, 303(1, 303/7, 357. BOB I nos. 551, 556, 578, 585, 608, 624, 625, 627, 647, 713 a, b, 738, 740. BOB II nos. 753, 754, 757, 768, 772, 773, 793, 796, 802, 811, 816, 818, 821, 822, 825, 827, 833, 839, 851, 862, 879, 890, 915, 918, 922, 943, 953, 957, 963, 964, 967, 980, 988, 989, 993, 1009, 1010, 1014, 1017, 1025, 1027, 1033, 1034, 1078, 1089, 1099, 1109, 1120, 1151, 1157, 1161, 1164, 1168. BOB I nos. 1197, 1203, 1208, 1210, 1211, 1218, 1222, 1223/1, 1225, 1227, 1229, 1238, 1244, 1246, 1247, 1248, 1249, 1256, 1263, 1268, 1271, 1272, 1276, 1279, 1280, 1288, 1290, 1292, 1294, 1295, 1298, 1299/2, 1303/1, 1309, 1310, 1324, 1325, 1327, 1329, 1332, 1335, 1344, 1345, 1346, 1349, 1350, 1352, 1353/1-7, 1354, 1356, 1361, 1363, 1371, 1386/1, 1388/1, 1392/1, 2, 1394, 1395, 1396, 1406, 1407, 1410, 1414, 1415, 1417, 1418. BOB nos. 2252 (1-12), 2255/1, 2259, 2260, 2291, 2297, 2322, 2373, 2394, 2395, 2410, 2413, 2435, 2438, 2445 (Holotype), 2446a, 2458, 2460, 2461, 2463, 2464 (Isotype), 2468 (1-5), 2473, 2492, 2494, 2504, 2510, 2514, 2519, 2521, 2524, 2525, 2541, 2553 (1-5), 2595, 2612, 2628, 2642, 2646, 2647, 2648, 2795, 2802, 2807, 2829, 2850, 2853, 3027.
- Muséum national d'Histoire naturelle Paris, Laboratoire de Paléontologie, France. *Fagus pristina*. Provence, southern France, 10 specimens, nos. 12710, 12784, 13057, 13059, 13060, 13069, Bois d'Asson; 13097 Fontienne; 13095, 13523 (non *Fagus*) Manosque. *Fagus castanaefolia*. Provence, southern France, Bois d'Asson, one specimen, no. 13069.
- Specimens belonging to Institute of Paleontology, University of Vienna; Geological Survey, Vienna; Paleontological collection Landesmuseum Joanneum, Graz – at present at Institute of Paleontology, University of Vienna. *Fagus attenuata*. Lintsching, Salzburg, Austria, five specimens, nos. 2867/201, 202, 203A, 204A, 205A. Fohnsdorf, Styria, Austria, two specimens, Fo1, Fo 2. Leoben-Seegraben, Styria, Austria, one specimen. Leoben, Styria, Austria, Holotype.
- Komarov Botanical Institute, Russian Academy of Sciences, Saint-Petersburg, Russia. *Fagus antipofii*. Kumsuat bay, Kazakhstan, 42 specimens, coll. 1016, nos. 1, 63b, 74b, 75b, 76b, 78, 79, 80, 81, 82, 83, 84a, 85, 86, 87a, 88, 89, 90, 91a, 93a, 94, 95, 96, 97, 98a, 99, 100, 101, 102b, 103, 103a, 104, 104a, 105, 106b, 107, 108, 109a, 134a, 138b, 145, 200a. Berekmyak, Urals, 15 specimens, coll. 971, nos. 37-47, 48a; coll. 29, no. 2 (1-3). Ashutas, Kazakhstan, 23 specimens, coll. 2113, nos. 19, 512, 634, 645, 654, 657, 683, 689, 695, 696, 704, 719, 722, 728, 732, 738, 798, 1007, 1559, 1567, 1569, 1586, 1595.

B. Oligocene to Middle Miocene *Fagus* from East Asia, North America, and Iceland.

- Swedish Museum of Natural History, Stockholm. *Fagus antipofii/evenensis/salnikovii*. Burdigalian, Makaryevka village, Sakhalin, four specimens, nos. S05937, S05939, S105940, S05941. *Fagus "antipofii"*. Middle Miocene, Alaska, English Bay, eight specimens, nos. S105918, S105919, S105920, S105921, S105923, S105923, S105925, S105928.

Fagus sp., 15 Ma, Selárdalur, northwestern Iceland, about 100 unnumbered specimens.

- Komarov Botanical Institute, Russian Academy of Sciences, Saint-Petersburg, Russia. *Fagus irvajamensis*. Lower Oligocene, Irvayam river, tributary of Podkagernaya river, northwestern Kamchatka, 5 specimens, coll. 1472, nos. 1, 2, 3, 4 (Paratype), 5. *Fagus evenensis*. Middle Miocene, Kavavlya river basin, Kamchatka, 30 specimens, coll. 1471, nos. 1a, 2, 3, coll. 1186, nos. 183, 184, 185 a & b, 186, 187 a, 188, 189 a & b, 190, 191, 192, 193, 194, 195, 196, 197, 198, 199, 200, 202, 203, 204, 205 a & b, 206, 207.
- Vernadsky State Geological Museum, Moscow, Russia. *Fagus irvajamensis*. Lower Oligocene, Irvayam river, tributary of Podkagernaya river, northwestern Kamchatka, of 18 specimens only 3 belong to *Fagus*, collections examined 6273, 5973, 7361. *Fagus evenensis*. Middle Miocene, Kavavlya river basin, Kamchatka, 63 specimens, coll. 720, nos. 8a, 9, 11, 14, 19, 20, 21, 22, 23, 32, 35a, 37, 43, 45, 47, 49, 50, 52, 53, 54, 56, 57, 58, 60, 74, 83, 91, 92, 187, 743, 1183, 1448, 1450, 1452 a & b, 1459, 1460, 1461, 1463, 1464, 1467, 1471, col. 725, nos. 47, 188, 189, 190, 191, 195.
- Paleontological Institute and Museum, Russian Academy of Sciences, Moscow, Russia. *Fagus salnikovii*. Upper Oligocene to Lower Miocene, Sakhalin, four specimens, coll. 3861, no. 132, coll. 3578, nos. 13, 15, coll. 3813, no. 8b-1.
- University of Florida, Florida Museum of Natural History, Gainsville, USA.

Fagus pacifica. Early Oligocene, Oregon, 14 specimens, nos. UF 15842-007008 to 007010, UF 00250-007035, UF 0258A-010214 and 010215, UF 0258A-010222, UF 00250-010597 and 010598, UF 00250-010636 and 010637, UF 00250-010776, UF 00250-010923, UF 00250-025197.

C. *Fagus gussonii*

- Swedish Museum of Natural History, Stockholm. Ellasona, south of Mt. Olympos, 30 unnumbered specimens. Vegora, northwestern Greece, specimens collected from 2000 to 2002, not all of them numbered; 160 numbered specimens, nos. S115957 to S115960. S115961 a & b, S115964, S115965, S115992 to S115999, S116000 to S116143. Makrilia, Crete, two unnumbered specimens.

Mókollsdalur, Iceland, 67 specimens, nos. S094771 to S094777, S094779, S094780, S094785, S094787, S094791 to S094794, S094795, S094799 to S094801, S094803 to S094808, S098813, S094816, S094817, S094821 to S094823, S094827, S094828, S094830, S094832 to S094834, S094840, S094844, S094845, S094848, S094849, S094851, S094953 to S094855, S094858, S094859, S094861, S094862, S094864 , S105944 to S105949, S105951 to S105957, S106893, S106894.

- Institute of Paleontology, University of Vienna, Austria. La Cerdaña, northern Spain, three unnumbered specimens.

D. *Fagus haidingeri*

- Swedish Museum of Natural History, Stockholm. Two specimens from Frankfurt-Niederrad, about ten specimens from Willershausen.
- Museum für Mineralogie und Geologie, Dresden, Germany. *Fagus kraeuselii*. Pliocene, Berga, Germany, 111 specimens, nos. BG 1, 2, 6, 13, 14, 15, 17, 19, 20, 23, 25, 27, 28, 30, 32, 34, 40, 42, 49, 55, 56, 58a, 65, 66, 68, 69, 73, 80, 85, 86, 90, 98, 105, 108, 114/1, 2, 118, 123, 128/1, 2, 130, 133, 135, 136, 141, 146, 148, 149, 151, 154, 160b, 163, 172, 173a, b, 174, 179, 180, 189, 210, 216, 272, 274, 275, 276, 280, 291, 293, 298, 312, 313, 324, 333, 334, 336, 341, 344, 352, 353, 356, 363, 364, 377, 378, 382, 385a, 391/1a, 396, 398, 401, 406, 417, 424, 426, 427, 432, 439, 445, 452, 455, 456, 457, 464, 465, 470, 471a, 479, 489a, 500, 506, 521.

Fagus silesiaca. Late Miocene, Sośnica close to Wroclav, Poland, one specimen, Isotype.

- Senckenberg Museum, Frankfurt-Niederrad, Germany. *Fagus kraeuselii* (*Fagus decurrens*, *Fagus pliocenica, Fagus ferruginea* var. *fossilis*). Pliocene, Frankfurter Klärbeckenflora, Germany, 81 specimens, nos. B11896 (KN70), B11897 (KN71), B11898 (KM74), B11899 (KN75), B11900 (KN8), B11901 (KN63), B11902 (KN67), B11903 (KN76), B11904 (KN4), B11905 (KN3), B11906 (KN2), B11907 (KN1), B11908 (KN9), B11909 (KN 20), B11910 (KN68), B11911 (KN7), B11912 (KN6), B11913 (KN5), B11914, B11915 (KN16), B11916 (KN15), B11917 (KN19), B11918 (KN18), B11919 (KN42), B11920 (KN61), B11921 (KN51), B11922 (KN17), B11923 (KN72), B11924 (KN36), B11925 (KN35), B11926 (KN60/59), B11927 (KN53), B11928 (KN58), B11929 (KN54), B11930 (KN73), B11931 (KN57), B11932 (KN41), B11933 (KN48), B11934 (KN45), B11935 (KN33/34), B11936 (KN30), B11937 (KN39), B11938 (KN37/38), B11939 (KN65), B11940 (KN21), B11941 (KN69), B11942 (KN32), B11943 (KN31), B11944 (KN47), B11945 (KN10), B11946 (KN11), B11947 (KN12), B11948 (KN16), B11949 (KN14), B11950 (KN66), B11951 (KN43), B11952 (KN44), B11953 (KN46), B11954 (KN52), B11955 (KN50), B11956 (KN49), B11957 (KN62), B11958 (KN20), B11959 (KN20), B11960 (KN29), B11961 (KN27), B11962 (KN28), B11963 (KN24), B11964 (KN22, KN23), B11965 (KN21), B11966 (KN25, KN26), B11967 (KN56), B11968 (KN40), B11969 (KN64), B11970 (KN77), B11971 (KN55).

Fagus. Pliocene, Neu-Isenburg, 23 specimens, nos. D 1 to D 23.

- Institut und Museum für Geologie und Paläontologie der Universität Göttingen, Germany. *F. kraeuselii* (*Fagus sylvatica*). Pliocene, Willershausen, Germany, 191 specimens, nos. 13, 15, 16, 24, 128, 193, 194, 217, 441, 443, 446, 449, 455, 456, 459, 461, 748, 3849, 5766, 6586, 9939, 10032, 10186, 10607, 11053, 11213, 11690, 12265, 12457, 12937, 12979, 12992, 13025, 13795, 13899, 14024, 14177, 14570, 14703, 14819, 15394, 15510, 15883, 16004, 16079, 16168, 16169, 16176, 16196, 16806, 16841, 17125, 17263, 17324, 17387, 17442, 17757, 17897, 17947, 18064, 18105, 18371, 18659, 19075, 19391, 19392, 19410, 19411, 19412, 19417, 19426, 19525, 19535, 19539, 19543, 19545, 19945, 19972, 20000, 20264, 20460, 21017, 21088, 21204, 21248, 21271, 21314, 21315, 21344, 21472, 21480, 21511, 21562, 21657, 21664, 21779, 21891, 22016, 22160, 22257, 22279, 22282, 22943, 23290, 23367, 23484, 24588, 30114, 30390, 30549, 30550, 30639, 30959, 30992, 38400, 10/414, 12937a, 14429a, 14476a, 15394a, 15989a, 16689a, 16693a, 17158a, 17685a, 17947a, 19418/1, 195-28, 19540a, 19541a, 19890a, 19945a, 20771a, 21497/1, 21497/2, 215a, 22-213a, 22312a, 22804a, 24716. 8822a, 36- 63, 37- 27a, 37/27b, 38- 407, 38/14, 38/147b, 38/399, 38/401, 38/402, 38404b, 39/112, 39/113, 39/214, 39/217, 39/6, 39/8, 412- 20, 441a, 46/109, 46/16, 46/55, 46/7, 47/19, 479- 21, 489- 9, 49/40, 51/50, 52-3556a, 57- 33, 762- 18, 818- 19, P38-1. 22632, P38-10. 8335, P38-11. 9284, P38-14. 2412, P38-15. 4165, P38-2. 2686, P38-3. 3559, P38-4. 3563, P38-5. 5140a, P38-6. 5923a, P38-7. 5971, P38-8 (1-4). 6932a, P38-12 (1-3). 4923, Wegele 01, Wegele 19390, Wegele 19548, Wegele 19549, Wegele 19550- 19547.

- Muséum national d'Histoire naturelle Paris, Laboratoire de Paléontologie, France. *Fagus pliocenica* (*Fagus sylvatica*). Pliocene, Cantal, central France, seven specimens, nos. 12449, and six unnumbered specimens.

- Specimens belonging to the Institute of Paleontology, University of Vienna; Geological Survey, Vienna; and private collectors, at present at the Institute of Paleontology, University of Vienna, Austria. *Fagus haidingeri*. Vienna, Lower Austria, Upper Austria, and Burgenland, Austria, specimens described in ZETTER 1984, about 30 specimens seen.

- Museum of Natural History, Ukrainian Academy of Sciences, Lviv, Ukraine. Swoszowice close to Cracow, Poland, six specimens, nos. PB-N 20, 45, 61, 66, 69, 71.

Kleparivs'ka Vysochyna, western Ukraine, 13 specimens, nos. PB-N 2009, 2034, 2052, 2119, 2126, 2137, 2149, 2150, 2151, 2153, 2159, 2160, 2162.

Kortumova Hora, western Ukraine, 80 specimens, nos. PB-N 88, 90, 92, 93, 94, 95, 96, 97, 100, 102, 108, 113, 113a, 122, 123, 136, 137, 139, 159, 190, 217, 257, 260, 313, 349, 358, 359, 367, 369, 371, 379, 380, 381, 393, 397, 409, 416, 418, 430, 438, 454, 472, 489, 504, 510, 511, 512, 513, 514, 518, 519, 520, 543, 557, 561, 592, 595, 601, 605, 673, 676, 683, 691, 694, 701, 711, 726, 749, 755, 756, 776, 777, 781, 786, 789, 790, 801, 815. Hlyns'ke, western Ukraine, one specimen, PB-N 904. Kosiv, western Ukraine, 41 specimens, coll. 1B, nos. "15b", "16b", "17b", "18b", PB-N 1250, 1251, 1255, 1256, 1257, 1258, 1259, 1265, 1266, 1267, 1268, 1269, 1270, 1271, 1274, 1275, 1276, 1277, 1278, 1279, 1280, 1285, 1286, 1288, 1289, coll. 1, no. PB-N 1318, coll. 22, PB-N 1452, coll. 23, PB-N 1507, 1509, 1510, 1512, 1513, 1514, 1515, 1545, 1583, 1585. Mychyn, western Ukraine, 44 specimens, coll. 9, PB-N 920, 923, 928, 931, 935, 936, 941, 942, 943, 946, 948, 949, 950, 951, 953, 955, 964, coll. 13, "102", "104", PB-N 989, 999, 1000, 1006, 1006a, 1008, 1014, 1033, 1033a, 1034, 1035, 1036, 1041, 1042, 1044, 1045, 1046, 1055, 1061, 1062, 1066, 1070, 1074, 1075, 1080. Velyka Uholka, western Ukraine, 27 specimens, coll. 29, nos. 18, 19, 22, 25, 27, 32, 36, 79, 102, coll. 53, nos. 2, 4, 10, 18, 19, 20, 35, 40, 44, 45, 63, 70, 74, 80, 97, 100, 101, 106.

- Komarov Botanical Institute, Russian Academy of Sciences, Saint-Petersburg, Russia. *F. orientalis fossilis*, Armavir, Northern Caucasus, southern Russia, 70 specimens, coll. 347a, nos. 7, 8, 9, 10, 24, 25, 26, 27, 28, 29b, 30, 33, 35, 40b, 41, 46, 47, 54, 58a, 62, 64, 65a, 65b, 67, 68, 69, 70a, 71, 72, 73, 74, 76, 77, 78a, 79, 90, 91, 115, 116a, 123, 124a, 130, 135, 148, 158, 171, 173, 182b, 183b, 185, 186, 187, 189, 191, 192, 193, 196a, 197, 200, 201, 208a, 212, 216, 217, 221, 222, 242, 243, 245, 307. Krynka, Northern Caucasus, southern Russia, 61 specimens, coll. 982, nos. 173a, 252- 256, 258, 259, 260, 262, 263, 264, 265, 267, 268, 269, 271, 273, 274, 275, 277-295, 298-313, 458, 459, 1073, 1076.

- Dipartimento di Scienze della Terra, University of Torino, Italy.

Villages Scaparoni and Castagnito, Piedmont, Italy, Late Miocene, 30+ specimens, nos. Sc/0090, Sc/0092, Sc/0119, Sc/0120, Sc/0131, Sc/0140, Sc/0142, Sc/0149, Sc/0157, Sc/0599, Sc/0601, Ca/0050, Ca1/0013, Ca2/0040, Ca2/0041, Ca2/0045, Ca2/0053, Ca2/0060, Ca2/0061. Valmanera, Piedmont, Italy, Pliocene, 10+ specimens, nos VALM 24, 29, 37, 39, 60, 87, 94, 103, 107. Cossato close to Biella, confluence of rivers Cervo and Strona, Pliocene, three specimens, nos. 279, 113, 112. La Cassa, Torino, Pliocene, 10+ unnumbered specimens.

F. Other Late Tertiary *Fagus* from East Asia

- Swedish Museum of Natural History. *Fagus stuxbergii*, Mogi, Japan, Pliocene, around 200 specimens.