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# THE TAXONOMY OF *FAGUS* IN WESTERN EURASIA AND THE ANCESTORS OF *FAGUS SYLVATICA* S.L.

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ABSTRACT. A considerable amount of variability within extant populations of *Fagus sylvatica* is caused by modification. In addition, morphoclines occur from W to the E as well as in a mosaic-like pattern. The European *F. sylvatica* ssp. *sylvatica* turns out to be morphologically homogeneous while the SW Asian *F. sylvatica* ssp. *orientalis* is more heterogeneous. N Iranian populations of ssp. *orientalis* show strong similarities to *F. grandifolia* ssp. *caroliniana* in S Georgia and Florida.

Ancestors similar to *F. sylvatica* already existed in the Pliocene (Frankfurt, Willershausen, Berga) and Upper Miocene (Iceland, Russia). The extant W-E gradient between ssp. *sylvatica* and ssp. *orientalis* seems not to have existed in the same way during the Pliocene. Upper Miocene beeches of Iceland (*F. antipofii*, leaves and cupules) as well as the Mediterranean *F. gussonii* resemble extant *F. sylvatica* ssp. *orientalis* of N Turkey and Transcaucasia. The genus *Fagus* can be characterised by an initial reticulate evolutionary phase, which resulted in morphological parallelisms.

KEY WORDS: *Fagus,* W Eurasia, reticulate evolution, parallelism

## INTRODUCTION

Though the genus *Fagus* is comparatively small, concepts on the species numbers within *Fagus* are controversial (Table 1). The present state-of-the-art is to treat European and W Asiatic beech taxa as only one species, *Fagus sylvatica*, the Common beech, which consists of two subspecies: ssp. *sylvatica* and ssp. *orientalis* (Greuter & Burdet 1981). The Moesian beech of the Balkans is supposed to be a hybrid between the latter two. Important characters to distinguish the European beech from the oriental beech are the appendages of the cupules and the number of secondaries. Both, ssp. *sylvatica* and ssp. *orientalis* are supposed to have entire leaf margins. Shen (1992) questioned the present concept and reestablished Hohenacker's beech, *F. sylvatica* ssp. *hohenackeriana*, which has been described by Palibin (1908) for Caucasia and Iran. Based on the current taxonomic concept of extant beeches the derivation of contemporary W Eurasiatic beech types from pre-Quaternary taxa turns out to be unclear (Kvaček & Walther 1991). Walther (1994) assumed European Tertiary beeches to have become extinct at the end of the Tertiary and according to this interpretation *Fagus sylvatica* should be of postglacial origin. The present paper is part of a study with the aim of critically revising extant taxa of *Fagus* in western Eurasia with emphasis on the phenotypic variability of leaves and cupules. Extensive field studies in Europe, Turkey, Transcaucasia and Iran have been undertaken by the author. The collected material of *Fagus* has been analysed morphometrically. Based on these investigations a number of Miocene and Pliocene fossil species and their relations to extant taxa were reevaluated.

## TAXONOMY OF EXTANT *FAGUS* IN WESTERN EURASIA

A considerable amount of morphological variability within *Fagus* is caused by modifications, which means the phenotypic response of the genus to particular environmental conditions. Characters, which are strongly influenced by modifications are the texture of leaves (sun leaves vs. shade leaves) the leaf margin (entire vs. dentate), size of the leaf and number of secondaries as well as the degree of pubescence. Naturally, modifications are the ”taxonomic noise” we have to deal with and must not be mistaken for specific characters (see Denk 1999a, b). In addition, a clinal transition of characters occurs from W Europe to N Iran (Table 2). According to my results most of the Bulgarian beech populations (*Fagus moesiaca*) fit well into the morphological range of *F. sylvatica* ssp. *sylvatica*. A hiatus only exists in the easternmost Bulgaria, where scattered populations bearing leaf-like, stalked appendages are to be found (eastern Stara Planina). Prominent leaf-like appendages get frequent in N Turkey but are less common in Georgia and north Iran. A second hiatus can be observed between Transcaucasian

**Table 1**. Different species concepts in the genus *Fagus*

| species of Fagus | China | Taiwan | S Korea | Japan | W Eurasia | N America | Total no. |
|---|---|---|---|---|---|---|---|
| Chang (1966) | 10 | 1 | (1) | (2) | (2) | (1) | 17 |
| Chang & Huang (1988) | 6 | 1 | (1) | (2) | (1) | (1) | 12 |
| Shen (1991) | 8 | 1* | 1* | 3 | 1 | 1 | 13 |

values in parentheses indicate species not included in the studies of Chang (1966) and Chang & Huang (1988)
* species also occurring in China

and north Iranian populations. While the size of the leaves decreases in north Iran, the number of secondaries considerably increases (Table 2). Particular character combinations prove to be suitable for the distinction of several population groups. One of these characters is the co-occurrence of particular leaf bases and leaf apices (=base/apex pairs). By measuring statistically confidential numbers of specimens clear trends can be shown for each population group (Table 2, Pl. 1). Outstanding population groups are to be found in the everhumid area of the Colchis along the eastern coast of the Black Sea and again in north Iran. Moreover, north Iranian populations show a strong similarity to SE North American beech types of *Fagus grandifolia* ssp. *caroliniana* (Pl. 1a). The subspecies *hohenackeriana* Shen, therefore, turns out to be heterogeneous, the demarcation line between population groups lying not only between northen Turkey and Caucasia, but also between Transcaucasia and north Iran. Considering several transitional states (morphoclines) I refrain from establishing subspecies and treat all these population groups as belonging to ssp. *orientalis*.

## THE TREATMENT OF FOSSIL BEECH TAXA

### PLIOCENE

Willershausen/Germany: Two main types of leaves can be observed. Broad ovate leaves and narrower, elongated leaves. They have been referred to as *sylvatica* and *grandifolia* types resp. (Tralau 1962) and as *F. pliocaenica* ssp. *willershausensis* and ssp. *multinervis* resp. (Knobloch 1998). Kvaček & Walther (1991) integrate both types into *Fagus kraeuselii* Kvaček et Walther. The leaf remains correspond well to the most common base/apex pairs in ssp. *sylvatica* (Pl. 1, figs a-h). Types as in Pl. 1, fig. i and Pl. 2, fig. o (Tralau's *grandifolia* Gruppe) are comparable to ssp. *orientalis*. Numbers of secondaries, types of leaf dentation as well as size and types of stomata (compare Kvaček & Walther 1991, Denk 1999a, b) are within the range of *F. sylvatica*. However, overall leaf shapes sometimes are typically rhombic-ovate, which is one of the most characteristic features of some extant eastern Asiatic species.

Berga/Germany: *Fagus kraeuselii* Kvaček et Walther. Leaf remains of Berga are more homogeneous. They bear acute bases together with either acute or acuminate apices. Leaf remains show weak dentation as to be found in *Fagus sylvatica*. In addition, overall leaf shapes are similar to extant ssp. *orientalis.*

Frankfurt Klärbeckenflora/Germany: *Fagus kraeuselii* Kvaček et Walther. Overall leaf shapes and numbers of secondaries are close to ssp. *sylvatica*. However, they show a more pronounced dentation compared to extant F. *sylvatica* (Pl. 1, figs e, f). Leaves as in the fossil assemblage of Frankfurt are similar to shade leaves and leaves of shrub-like individuals of *F. sylvatica*, which often represent modified leaves (see above). Again the occurrence of "E Asiatic" leaf shapes, together with "European" ones and connected by morphological transitions, has to be mentioned.

### UPPER MIOCENE

Mokallsdalur/Iceland (Pl. 2, fig. p): *Fagus antipofii* (leaves and 2 impressions of cupules) Leaves are very similar to extant beeches in northen Turkey and Transcaucasia. Moreover, the two cupules have the same dimensions as in extant *F. sylvatica*. Other Upper Miocene beech remains comparable to extant ssp. *orientalis* are *Fagus juliae* Jakubovskaya (Pl. 2, fig. n), south-east of Moscow, and *Fagus gussonii* Massalongo, Mediterranean area.

## CONCLUSION

Upper Miocene and Pliocene beech types, which have been analysed, obviously display a mosaic pattern of characters. These characters partly reappear in extant taxa of western Eurasia (*F. sylvatica* ssp. *sylvatica, F. s.* ssp. *orientalis*), East Asia (overall leaf shape in some specimens of Frankfurt and Willershausen; *F. longipetiolata, F. bijiensis, F. hayatae* ssp. *hayatae, F. h.* ssp. *pashanica, F. tientaiensis, F. lucida* and *F. crenata*) and to a lesser extent of south-eastern North America (*F. grandifolia* s.l). Such phenomena and the close resemblance of easternmost populations of *F. sylvatica* ssp. *orientalis* to south-eastern North American beech types (*F. grandifo-*

**Table 2**. Clinal transitions of morphological characters. **a:** Leaf and cupule characters. Leaf Index = length / width × 100; l = length; **b:** Leaf characters; **c:** Cupule characters. type 1 = bud-scale homologous, brownish membraneous appendages. type 2 = small appendages, spathulate with acute to rounded apex, green turning brown. type 3 = prominent appendages, spathulate with acute to rounded apex, semi-evergreen. Note, that E Bul indicates scattered populations in the easternmost Stara Planina, which are supposed to be outposts of *Fagus sylvatica* ssp. *orientalis* or hybrids between the two subspecies *sylvatica* and *orientalis*; **d:** Leaf characters. * = almost oblong obtuse base, see Plate 2, fig. k. SW = SW Europe; Aut = Austria; Bul = Bulgaria; Bes = Puertos de Beceite, relictual stand of *Fagus sylvatica* ssp. *sylvatica* in E Spain, S Catalonia

**a**

| | | **leaf length** (mm) | | **cupule peduncle** (mm) | | **cupule length** (mm) |
|---|---|---|---|---|---|---|
| | Leaf Index * | l max | l mean | l max | l mean | l mean |
| **SW Europa**<br>n= 2000 | 154.6 | 110 | 57.76 | 30 | 11.76 | 19.83 |
| **Beseite**<br>n = 150 | 163 | 96 | 50.46 | 30 | 11.76 | 19.83 |
| **Austria**<br>n = 300 | 148.7 | 120 | 67.63 | 30 | 11.76 | 19.83 |
| **Bulgaria**<br>n = 2000 | 170.45 | 151 | 75.16 | 41 | 10.54 | 22.39 |
| **Turkey**<br>n = 800 | 196 | 172 | 85.50 | 75 | 25.01 | 22.32 |
| **Georgia**<br>n = 1000 | 187 | 187 | 78.49 | 66 | 19.12 | 20.16 |
| **Iran**<br>n = 1000 | 188 | 161 | 77.13 | 48 | 17.10 | 17.06 |

**b**

| **no. of secondaries** (%) | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | <7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | >15 |
| **SW Europa**<br>n= 2000 | 27.8 | 25.6 | 22.9 | 9.9 | 3 | 0.4 | 0.4 | 0 | 0 | 0 | 0 |
| **Beseite**<br>n = 150 | 19.3 | 39.2 | 26.9 | 11.5 | 3.1 | 0 | 0 | 0 | 0 | 0 | 0 |
| **Austria**<br>n = 300 | 15.4 | 11.7 | 24.5 | 29.6 | 17.8 | 0.7 | 0.3 | 0 | 0 | 0 | 0 |
| **Bulgaria**<br>n = 2000 | 17.9 | 17.9 | 21.2 | 17.5 | 16.3 | 7.1 | 2.1 | 0 | 0 | 0 | 0 |
| **Turkey**<br>n = 800 | 8.8 | 9.9 | 16 | 18.5 | 17.4 | 13.9 | 10.2 | 3.6 | 1.6 | 0.1 | 0 |
| **Georgia**<br>n = 1000 | 6.4 | 8.3 | 15.5 | 17.4 | 17.3 | 12 | 9.8 | 7.2 | 3.2 | 2.2 | 0.7 |
| **Iran**<br>n = 1000 | 2.9 | 3.4 | 8.3 | 14.7 | 16.6 | 18.2 | 16.5 | 12.3 | 5 | 1.7 | 0.4 |

**c**

| **frequency of prevailing basal appendages types** (%) | | | | | | | |
|---|---|---|---|---|---|---|---|
| type | SW | Bes | Aut | E Bul | Turkey | Georgia | Iran |
| 1 | 93.2 | 93.2 | 93.2 | 38.2 | 3.5 | 29.1 | 31.9 |
| 2 | 4.5 | 4.5 | 4.5 | 1.6 | 9.3 | 35 | 36.7 |
| 3 | | | 1.5 | 49.7 | 87.2 | 10.4 | 0.8 |

**Table 2**. Continued

**d**

**prevailing base/apex pairs within population groups of** *Fagus sylvatica*

| SW |  | Aut |  | Bul |  | Turkey |  | Georgia |  | Iran |  |
|---|---|---|---|---|---|---|---|---|---|---|---|
| base / | apex | base / | apex | base / | apex | base / | apex | base / | apex | base / | apex |
| obtuse | acute | obtuse | acute |  |  |  |  |  |  |  |  |
| acute | acute | acute | acute | acute | acute | acute | acute |  |  |  |  |
|  |  |  |  | acute | acuminate | acute | acuminate |  |  |  |  |
|  |  |  |  |  |  | obtuse | acuminate | obtuse* | acuminate |  |  |
|  |  |  |  |  |  |  |  |  |  | cordate | attenuate |

*lia* ssp. *caroliniana*) can be explained by the evolutionary mode of the genus. During an initial reticulate evolutionary phase *Fagus* inhabited a vast holoarctic area, ranging from Europe, via Siberia and north Asia, to western North America. Immense rates of gene flow then set up the conservative mode of evolution. Subsequently isolation of areas (disjunctions) and diversification of environments favoured speciation processes. However, due to the stenoecious behaviour of *Fagus*, few diagnostic characters were established. This stands in contrast to other genera (such as *Quercus, Acer* etc.), which diversified in an evolutionary phase of adaptive radiation, establishing well distinct species in heterogeneous environments.

The occurrence of parallelisms between extant and fossil beech types proves to be one of the characteristic features of the genus *Fagus*. European Tertiary beeches underwent gradual changes. This process was not stopped by the Pleistocene period. However, particular morphotypes of the Pliocene ancestors of *Fagus sylvatica* have been selected to recolonize Europe during the Postglacial period (Pl. 1, figs. a, b, c, d). Therefore, the present west-eastern gradient within the range of *Fagus sylvatica* is supposed to be of postglacial origin. Morphotypes comparable to both, *F. sylvatica* ssp. *sylvatica* and *F. sylvatica* ssp. *orientalis* already existed during the Pliocene and Miocene.

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# PLATES

Plate 1

a. *Fagus kraeuselii*, Will P38-12, 4923 (128/82) = Plate 1 in Tralau, 1962
b. *Fagus sylvatica* ssp. *sylvatica*, no. 797338, N Spain, San Sebastian
c. *Fagus kraeuselii*, Will 28217 (72+/31)
d. *Fagus sylvatica* ssp. *sylvatica*, no. 797096/2, S France, Mass. de la Ste. Baume
e. *Fagus kraeuselii*, F B11905 (74+/38)
f. *Fagus sylvatica* ssp. *sylvatica*, Austria, Styria
g. *Fagus sylvatica* ssp. *sylvatica*, no. f025, Austria, Southern Alps
h. *Fagus kraeuselii*, Will 38/401 (101/47)
i. *Fagus kraeuselii*, Will P38-15, 4165 (80+/41) = Plate 4, fig. c in Tralau, 1962, "*grandifolia*" Gruppe

Will = Willershausen (specimens housed in the Institut und Museum für Geologie und Paläontologie der Universität Göttingen), F = Frankfurt (specimens housed in the Naturmuseum und Forschungsinstitut Senckenberg, Frankfurt), values in parentheses = length /width in mm; nos. of recent specimens = coll. no. Herbarium T. Denk.

Plate 1

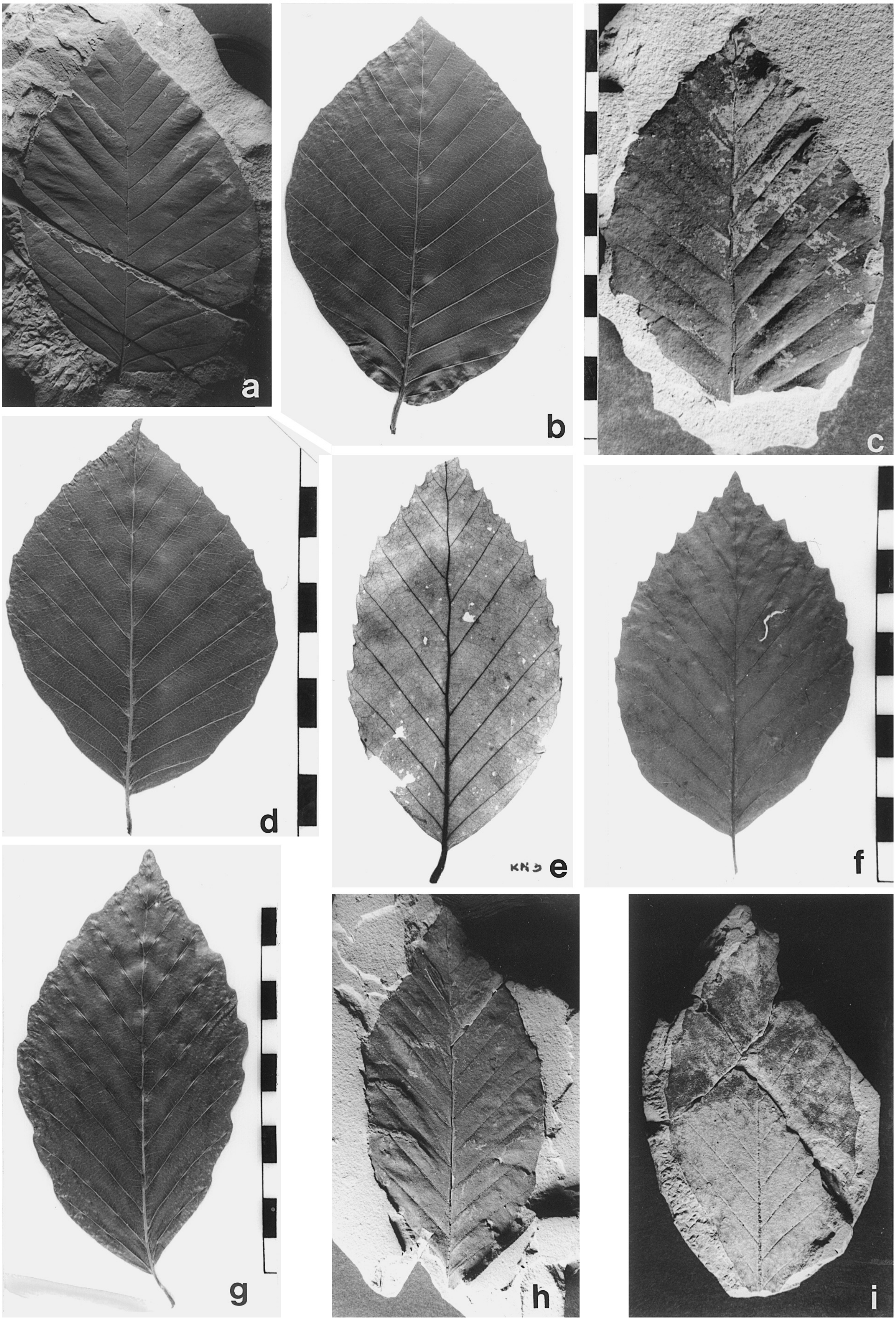
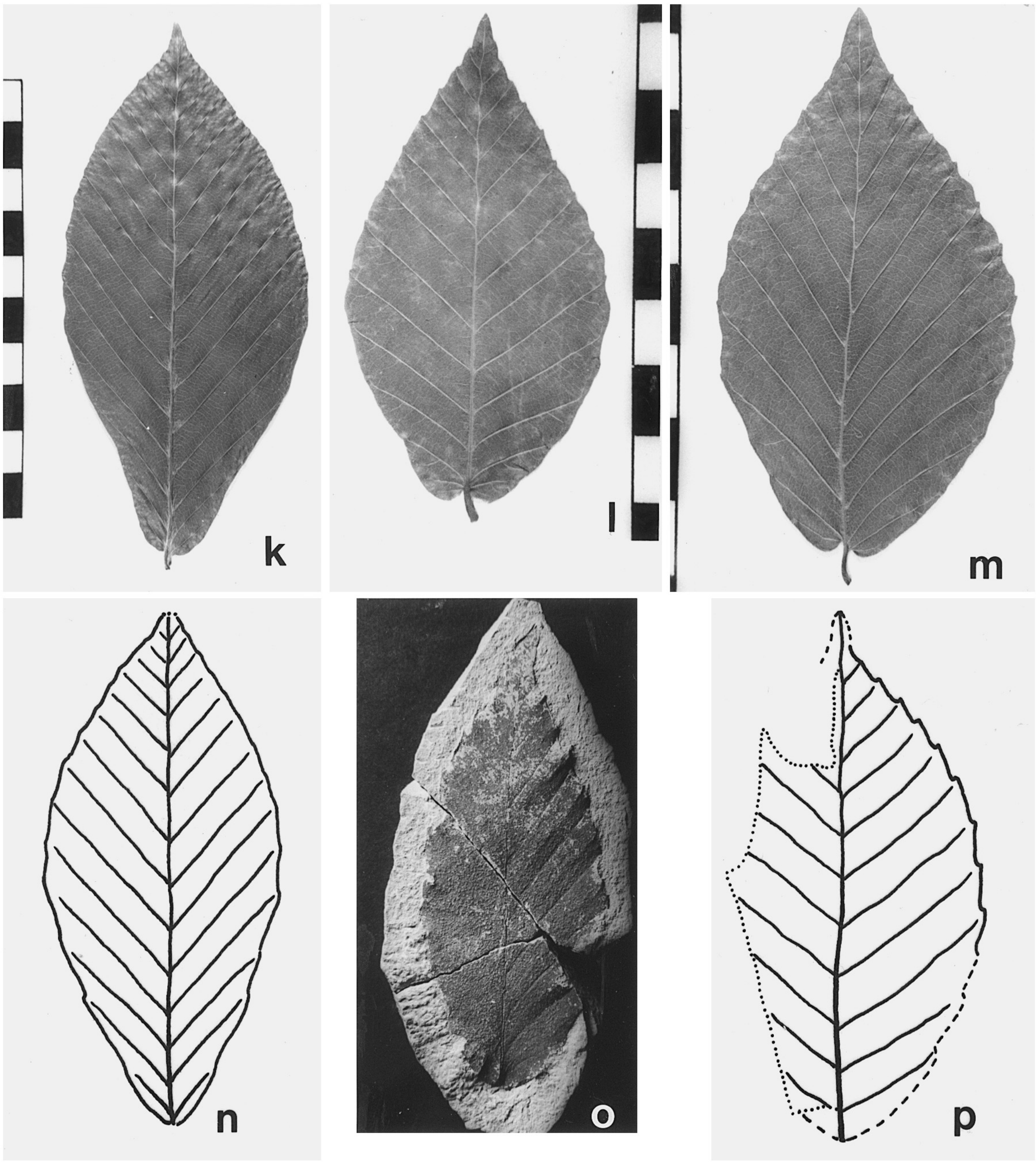


Plate 2

k. *Fagus sylvatica* ssp. *orientalis*, no. 896134, W Georgia, Colchis
l. *Fagus sylvatica* ssp. *orientalis*, no. 169961, Iran, Prov. Gilan
m. *Fagus grandifolia* ssp. *caroliniana*, no. 26497, USA, N Florida
n. *Fagus juliae* Jakubov., 0.8× = Pl. 57, fig. 9 in Takhtajan, 1982
o. *Fagus kraeuselii*, Will P38-14. 2412 (71+/28) = Plate 4, fig. b in Tralau, 1962, "*grandifolia*" Gruppe
p. *Fagus antipofii*, S105947 (80+/46), Iceland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