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A monograph of the genus *Fagus* Tourn. ex L. (Fagaceae)

Shen, Chung-Fu, Ph.D.

City University of New York, 1992

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A

A MONOGRAPH OF THE GENUS FAGUS TOURN. EX L. (FAGACEAE)

by

CHUNG-FU SHEN

A dissertation submitted to
the Graduate Faculty in Biology
in partial fulfillment of the requirements for
the degree of Doctor of Philosophy,
The City University of New York

1992

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BY

CHUNG-FU SHEN

1992

This manuscript has been read and accepted for the Graduate Faculty in Biology in satisfaction of the dissertation requirement for the degree of Doctor of Philosophy.

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Abstract

A MONOGRAPH OF THE GENUS FAGUS TOURN. EX L. (FAGACEAE)

by

Chung-Fu Shen

Adviser: Professor Arthur Cronquist

Thirteen species, and seven additional subspecies of five species, are recognized and described. One species (F. okamotoi) and one subspecies (F. japonica subsp. angustifolia) are new to science. Five new combinations at the subspecific level are made. Two subgenera (Engleriana subgen. nov. and Fagus) are recognized. Within subgenus Fagus, four sections (Longipetiolata sect. nov., Lucida sect. nov., Grandifolia sect. nov., and Fagus) are described. The work was conducted in the New York Botanical Garden. Close to five thousand specimens were assembled from 25 herbaria in Northern Hemisphere: East Asia (seven), Europe (six), and North America (12).

Descriptions of the genus and all recognized infrageneric taxa are provided, and taxonomic keys are also provided. The features concerned in these works are gross features observable under a x30 lens, but micro-features of leaves are also mentioned briefly in discussions at higher taxonomic levels. Discussions and speculations on ecology, evolution, and phylogeny are also significant constituents of the

present work. A specimen-citation list, 20 plates showing gross features, and 10 distribution maps appear as appendices.

The East Asian subgenus *Engleriana* is characterized by its "bush-like" tree-shape and many vegetative features. The differences among its four constituent (sub)species are chiefly in expressions of features of cupule/nut complex.

The East Asian section *Longipetiolata* (four species) is unique within the genus in its stout, blunt buds and papillate-glaucous lower leaf-surface. It shows a certain affinity to sections *Lucida* and *Grandifolia*. The four species of the other East Asian section *Lucida* have developed a clear pattern or tendency in their evolution of leaves. The three subspecies of each of *F. sylvatica* and *F. grandifolia* all have prominently winged nuts.

A clear evolutionary pathway of cupule-appendages from scale-like, through subulate, to thread-like, is seen in subgenus *Engleriana* and section *Lucida*. Specialized spathulate-foliaceous appendages occur in four of the five major subdivisions of the genus, except in section *Longipetiolata*. The supposed evolution in ecological adaptation is generally compatible with the taxonomic differentiation within subgenus or sections.

DEDICATED TO MY MOTHER-IN-LAW

HU CHIN-HSIA

THE NEW TAXA AND NEW COMBINATIONS INCLUDED IN THE FOLLOWING PAGES

INDICATE MY INTENT FOR FUTURE PUBLICATION;

THEIR APPEARANCE IN THIS DISSERTATION

IS NOT INTENDED TO CONSTITUTE FORMAL PUBLICATION

UNDER THE INTERNATIONAL CODE OF BOTANICAL NOMENCLATURE.

ACKNOWLEDGEMENTS

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POSTSCRIPT:

Five days after he approved the final version of the present dissertation, my mentor Arthur Cronquist died of a heart-attack on March 22 (Sunday), 1992, while he examined specimens in the herbarium of Brigham Young University.

March 24, 1992

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A MONOGRAPH OF THE GENUS FAGUS TOURN. EX L.

CHAPTER 1

INTRODUCTION

Although it has been said that "The homogeneity of this genus has apparently made it an unattractive candidate for monography." (Jones, 1986: 229), there have been at least two unpublished monographs of Fagus. The first one is said to be in completed form, written by I. V. Palibin around 1930 (mentioned and cited in Czechtott, 1932: 364). The second one, prepared by W. H. Camp after the Second World War, was never completed. Handwritten drafts and typescripts of Camp's work under various titles or unnamed, and handsomely prepared line-drawings of all recognized species, are preserved in the archives of the New York Botanical Garden Library, Bronx, New York, U.S.A.. Camp is probably the person who has annotated the greatest number of specimens of beeches growing outside the land where the botanist lives, followed by Palibin. OKAMOTO Motoharu (Osaka Museum of Natural History, Japan) has clearly expressed an interest in the subdivision of Fagus down to the subgeneric and sectional levels (pers. comm., 1989 March).

In terms of the number of species, the genus Fagus is far better represented in East Asia than in either West Eurasia or North America. There are two well-known species in Japan, and four in China. Chang (1966) revised, and Chang & Huang (1988) commented on, the Chinese species.

The gross morphology of flowers and inflorescences of species of Fagus is so uniform that roughly speaking any species can provide enough information for describing the whole genus. Traditionally, leaves, cupules, and nuts are among the most useful features in distinguishing species within Fagus, if not the only ones, just as in almost all other fagaceous genera. Some other features have been picked up and regarded as useful in delineating species by some authors. Unfortunately, they are of limited value. Some show the same obvious but repetitious variation between species (such as tree-form, see Rehder & Wilson, 1916: 191). Others were subsequently found to vary within the taxa under enquiry (such as the color of trichomes on the upper portion of perianth-tubes of male flowers, see Wulff & Zyrina, 1924: 278; Alden, 1986: 52). With the understanding that "Species are the smallest groups that are consistently and persistently distinct, and distinguishable by ordinary means." (Cronquist, 1988: 71), I have struggled to explore useful gross features. A stereo-microscope with a 30x magnification is enough for checking all features discussed in this monograph.

About one thousand and five hundred scanning electron microscope (SEM) photographs have been taken on dozens of samples of pollen and leaf. Dozens of microslides have also been prepared for observation on various leaf microfeatures. The SEM pollen morphology generally did not prove very beneficial for delineating beech species, but is useful in marking some subspecies recognized herein and in supporting a general evolutionary scheme of the living beech species deduced from my studies on gross morphology. Leaf surface microfeatures, particularly those of the stomatal complex, powerfully support the integrity of the taxa of

various levels treated herein: species composed of recognized subspecies, sections (incorporating series), and subgenera. TANAI Toshimasa (Dept. Geol. Miner., Hokkaido Univ., Japan) is presently conducting leaf venation analyses on beeches. My work in this respect indicates that leaf venation pattern may be as useful as SEM pollen morphology in beech research.

The taxonomic history of the genus Fagus, and that of individual infrageneric taxa, will be reported under corresponding subheadings of the subsequent chapters.

The gross morphology of leaves and cupule-appendages prove to be among the most important and useful taxonomic features at the specific level. The leaves borne on the middle portion of the current-year shoot and sometimes the cupule-appendages borne on the middle portion of the cupule-valves can well characterize species or subspecies. Sometimes the basalmost appendages provide especially useful taxonomic and evolutionary information, because it appears that evolutionary innovation begins with these lower appendages and proceeds to the upper ones. Therefore, in the descriptions, keys, and discussions, I refer to these middle leaves and middle cupule-appendages, unless otherwise indicated. The leaves of seedlings, sprouts and suckers are also excluded from such considerations. Counts of the number of secondary veins refer to the number on one side of the midrib only.

Names and identifications of the following attributes are to be considered in the present monograph: those validly published at or higher than the varietal rank, those considered as biologically meaningful, and those marking the "new and interesting things to

science" from poorly explored geographic regions. Subspecies is here employed as the only infraspecific rank worthy of taxonomic consideration. Because of the importance of field observations, for which I have had only a limited opportunity, I do not here attempt infraspecific organization below the rank of subspecies. Due to the almost world-wide distribution of the genus and the amazing variability of some wide-ranging species, further division of subspecies might better be accomplished by local investigators.

In my taxonomic treatment, a list of synonyms with information about the original citation of collections is presented immediately after the accepted specific name and before the description. Information and discussion on the type or lectotypification of the accepted name is provided immediately after the description. Names of the authors responsible for the Latin names of all taxonomic ranks are cited according to the "Draft Index of Author Abbreviations, 1984 Ed." whenever possible. All of the collection dates when expressed in Arabic figures are in the following order: year-month-day. All collection localities are presented in the following format: country, province/state-county.

CHAPTER 2

DESCRIPTION, NOMENCLATURE, AND AN INFRAGENERIC KEY FOR THE GENUS

2-1 DESCRIPTION

FAGUS Tourn. ex L. (1753 May), Sp. Pl.: 997.

DECIDUOUS TREES; high-branching, straight, stout, and to 40 m tall (most spp.), or low-branching, with several major trunks, and to 25 m tall (a few spp.). OUTER BARK very thin; generally smooth and shiny silvery; whitish and densely beset with smaller and rounded lenticels (most spp.), or slightly yellowish and more prominently speckled with larger and otherwise-shaped lenticels (a few spp.). CURRENT-YEAR SHOOTS often zig-zag; generally glabrous; with many prominent, whitish and rounded lenticels. LEAF-SCARS semi-orbicular. WINTER-BUDS single; axillary, the twig without a morphologically true terminal bud; fusiform (at most slightly 4-angled); 5-15-(20) mm long by the end of the growing season; consisting of many imbricate BUD-SCALES which are thick-chartaceous, reddish-brown to chestnut-brown, and ciliate at least along the upper margin. VERNATION conduplicate-plicate. LEAF-UNFOLDING in middle April to early May, depending on the taxon; immature leaves always covered with long, silky hairs, and nearly always (except in F. brevipetiolata) with tiny, yellowish-reddish glandular hairs on the lower leaf-surface. LEAVES simple; generally densely displayed

particularly on individuals with small leaves; alternate-distichous; (obovate), (obtrullate), (rhombic), elliptic, oblong, ovate, (lanceolate), or (trullate); (5)-8-12-(15) cm long; thin- to thick-chartaceous; at least when very young densely covered with long, whitish, unicellular, silky hairs. **APEX** acute to acuminate. **BASE** cuneate to rounded. **UPPER SURFACE** light green to dark green; often with persistent long hairs on the major veins. **LOWER SURFACE** concolored with upper surface (most spp.) or glaucous (a few spp.); often with long, persistent hairs on the major veins; sometimes with short, eglandular hairs on the inter-veinal areas. **MIDRIB** slender; often zig-zag toward the apex; slightly elevated above or level with upper surface. **SECONDARIES** (5)-8-15-(20); level with upper surface; straight at least along their earlier 4/5 course, then either straightforward ending into a tooth-tip, or abruptly curving upward when closely approaching margin, or taking an intermediate situation in which an upward branch leaves the end portion of the secondary that will terminate a tooth-tip. **INTERSECONDARIES** absent. **TERTIARIES** percurrent; roughly perpendicular to the secondaries. Primary/secondary-axillary **POCKET-DOMATIA** normally filled with a hair-tuft present in most species. **MARGIN** slightly sinuous, denticulate, or serrate. **SINUSES** when present convex, undulate, straight, or concave. **PETIOLE** generally ca. 1/8-1/12 as long as leaf-blade. **STIPULES** multiveined; when modified into bud-scales (the most common condition) caducous, oblanceolate, 1-2 cm long, membranous in the lower portion but becoming chartaceous upward; when associated with proleptic leaves more or less persistent, ovato-lanceolate or ovate with a long apiculate apex, 0.5-1 cm long, membranous. **LEAF-FALL** in

late October to November.

ANTHESIS in middle April to early May, depending on the taxon. (MAST YEAR occurring every 3-5 years.) **FLOWERS APPEARING SIMULTANEOUSLY WITH LEAVES. MONOECIOUS; PROTOGYNOUS and WIND-POLLINATED. MALE INFLORESCENCES** capitate (globose); small (ca. 1 cm in diam.); axillary to more proximal leaves; single; pendulous; with a long (3-6 cm), hairy, very slender, and flexuose peduncle, which always has 1-4 caducous bracts on the upper portion. Flowers per male inflorescence up to 40; very crowded. **MALE FLOWERS** whitish to yellowish; with short (0.5-2 mm), very thin, and hairy pedicel. **PERIANTH-TUBE** campanulate; membranous; hairy on the outer surface; 3-5 mm long; 5-8-lobed. **STAMENS** (8)-10-12-(16). **FILAMENTS** very slender; 4-5 mm long. **ANTHERS** generally exerted from the perianth-lobes; oblong to elliptic; 1.5-2.0 mm long; generally with a tiny and inconspicuous connective-tip. **FEMALE INFLORESCENCES** axillary to the more distal leaves, represented by 2 subterminal flowers which are enclosed by a ((3))-4-valved cupule, which is atop a **CUPULE-PEDUNCLE** which has 1-4 bracts near the top. **FEMALE FLOWERS** 3-carpellate; sharply 3-angular in cross-section at anthesis. The 6 lobes of the **PERIANTH-TUBE** green; chartaceous; hairy; arranged in 2 whorls of 3 each. **STIGMAS** 3; distinct; long-lanceolate; spreading; persistent; with the entire inner surface reddish and stigmatic at anthesis. **FRUIT MATURING** in middle July to late August of the current year, depending on the taxon. **CUPULE-VALVES** distinct throughout ontogeny; with the inner surface tomentose. **CUPULE-APPENDAGES** scale-like, thread-like (=linear), or spathulate-foliaceous in different taxa, often recognizable to the specific level even immediately after pollination. The 2 **NUTS** equal in

shape and size, roughly maintaining the general shape of flowers. Wing-like and membranous outgrowth along the upper portion of each nut-angle normally present in many species. Nuts either level with the cupule-valves or exserted to various degrees. **NUT-SCARS** sharply 3-angular (most spp.) or rounded (few spp.). The 2 **COTYLEDONS** oily; folded together (plicate) into a generally rather complex pattern. **SEEDS** germinating epigeally the following spring.

TYPE SPECIES:

"**Fagus (sylvatica)** foliis ovatis obsolete serratis. Habitat in Europa."

L. (1753 May), Sp. Pl.: 998. **LECTOTYPIFIED** by Britton & Brown, 1913

June, Ill. Fl. N. U. S. Canada, ed. 2, 1: 614.

CURRENT DISTRIBUTION:

HORIZONTAL: Disjunct in the following three regions: **EAST ASIA** (Japan, Korea (Ulreung Isl. only), China, and Vietnam), **WEST EURASIA** (westernmost Ukraine, Azerbajdzhan, Armenia, Gruzija, Iran, Turkey, United Kingdom (Great Britain only), and all European continental countries except Portugal, Finland, the three Baltic states, and Bjelorussija), and **EASTERN NORTH AMERICA** (Canada, U.S.A., and Mexico). North to ca60 degrees N (in NW Europe). South to ca. 19.5 degrees N (in Mexico).

ALTITUDINAL: From sea-level (in its northern range) to higher than 2,000 m (to 2,500 m) (in central China, Caucasus, Alps Mts., and Mexico).

DISTRIBUTION MAPS: See Tanai (1974: 66), Yim (1983: 156), Chang & Huang (1988: 112); among others.

HABITAT AND ECOLOGY:

AUTECOLOGY: Beeches grow in localities of the Northern Hemisphere with a climate ranging from cool subtropical to warm cool-temperate. When they are present in localities well within the subtropical climatic region, they grow in montane regions higher than 1,500 m. When they are present in localities well within the cool-temperate climatic region, they grow in lowlands near sea-level. Ecological differences between species, even sympatric ones, are not prominent. In terms of temperature, beeches are generally found in localities with the average July temperature between 20 and 27 degrees C, and the average January temperature lower than the freezing point. In terms of precipitation, they need a growing-season rainfall of no less than 500 mm. A high relative humidity often characterizes the habitat of beeches. [Beeches have a very thin outer bark, if it is present, and hence are very susceptible to fire damage. An often foggy habitat can act as a "security-guard" for beeches.] Most probably all beech species have symbiotic ecto-mycorrhizae (as probably do all other fagaceous plants); this partly explains the very broad range of soil types on which beeches are found, though they perform best on acidic loams. The pH value of soils on which beeches can grow ranges from 3 to 7. Nevertheless, limestones and calcareous soils are among the most common substrata on which beeches are found. The soils on which beeches thrive must be well drained. Many beeches have their root-systems expanding nearly horizontally at very shallow soil levels; they are therefore very susceptible to wind-fall. Some eco-races of some beeches are dwarfed

and/or prostrate to some extent and occupy very harsh and/or very windy habitats. Tree-gaps created by wind-fall are very important in the natural regeneration and maintenance of some beech forests. A few East Asian species can regenerate by the vigorous growth of new shoots from their multi-branched stumps after clear-cutting. Many beeches produce root- and/or stem-suckers, which sometimes function in natural regeneration. Probably because of the ectomycorrhizal habit, broad range of soil adaptation, and chiefly horizontally developed shallow root-system, many beeches thrive on steep slopes and/or limestone ridges, where sometimes no other trees seem to outcompete them.

SOCIOECOLOGY: Beeches are forest inhabitants. Pinaceous conifers, cold-tolerant evergreen trees, and thermophilic deciduous trees are present in various combinations in different localities where beeches are common. In their southern range (in mountains), they are mostly members of the so-called "mesophytic forest". In their northern range (on plains), they are mostly elements of the so-called "northern hardwood forest" or its equivalent. When and where the environments allow, they form pure or near-pure stands of their own; these beech stands are sometimes contiguous or very extensive and cover a large area of landscape. Seedlings and saplings of beeches are very shade-tolerant; this partly explains the predominance of beeches in many forest associations. Some beeches are said or proved to release toxic materials into soils through the natural disintegration of their leaves. This allelopathic behavior can at least partly explain the very poor development of the herbaceous layer in some northern beech forests. In contrast, a very dense layer of dwarf bamboos is characteristic to

almost all East Asian beech forests.

SELECTED REFERENCES: WORLD-WIDE: Yim (1983). **EAST ASIA:** Anonymous (1980); Chang & Huang (1988); Chen et al. (1965); Haemet-Ahti et al. (1974); Hsieh (1989); Kim et al. (1986); Liu & Su (1972); Ohkubo et al. (1988a); Peters (1988); Peters & Ohkubo (1990); Sasaki (1970); Tsien et al. (1975); Wang (1961); Wolfe (1979); Yang (1978); Yim et al. (1980); Yoshioka (1937a, 1937b, 1938); Wu et al. (1980). **WEST EURASIA:** Bottema (1988); Browicz (1982); Eschrich et al. (1989); Grime et al. (1988); Hjelmqvist (1940); Kayacik & Yaltirik (1971); Lichtenthaler et al. (1981); Milesescu et al. (1967); Pacyniak (1971); Ruebel (1932); Wilson & Harley (1983). **E NORTH AMERICA:** Braun (1950); Brewer & Merritt (1978); Camp (1951); Forcier (1975); Fowells (1965); Haines (1965); Held (1983); Hernandez-X. et al. (1951); Jones & Raynal (1986); Koop (1987); Logan (1973); Miranda & Sharp (1950); Nesom & Treiber (1977); Rudolf & Leak (1974); Rushmore (1961); Russell (1953); Ware (1978); Whittaker (1956); Williamson (1975); Woods (1979).

DERIVATION OF THE GENERIC NAME, AND LOCAL NAMES OF FAGUS SPECIES:

The word "fagus" is the Latin translation of an ancient Greek word "phagos" (in turn, "phagein" = to eat). It refers to the edible and delicious beechnuts of the common European beech, which were consumed by the ancient people inhabiting southern and southeastern Europe. Beech is the English name of the common European beech. The several beech species growing in China are generally collectively called Shuei-Ching-Gang or Ching-Gang, among numerous local names. Beeches growing in Japan (at least two species are represented) are called Buna.

USES:

Because of the large size of the trees and their abundance in many regions, beeches often provide the most common timber. The great hardness and toughness of beech wood make it good material for making tool-handles, wheel-cobs, railroad-ties, boat-keels, floors, and furnitures, utensils, etc. Because beechwood tends to warp easily and is not durable, it is often inexpensive. Beechwood is also frequently used as a good fuel or for making high-quality charcoal. Beechnuts are oily and delicious; sometimes they are pressed for oil, or used for fattening pigs and poultry. In the wild, beechnuts are welcomed by various animals. In some regions beeches are an important cultural element because of their beauty and popularity. The smooth and whitish/silvery bark of many beech species makes it among the best subjects for juvenile inscription. Beech barks were often used for writing in ancient Europe. This traditional use of beech bark is said to have led to the origin of an important word: book, in Germanic culture.

SELECTED REFERENCES: **EAST ASIA:** Anonymous (1980); Hayashi (1969); Ohba (1989); Yang (1978). **WEST EURASIA:** Garrett-Fawcett (1885); Friedrich (1970); Loudon (1854); Woodbury (1923). **E NORTH AMERICA:** Betts (1943).

2-2 NOMENCLATURE

Most earlier authors cited Tournefort as the author of the

generic name Fagus. In his "Institutiones rei Herbarie" (1700: 584), Tournefort wrote: "Fagus est plantae genus, flore amentaceo A, glomerato D, plurimis nempe staminibus B constante e calyce C campaniformi surgentibus: Embryones autem E in eadem arbore a floribus separati nascuntur F abeuntque in fructum G callosum, acuminatum, quadrifariam apice dehiscentem H, binis plerumque seminibus foetum I, K trigonis L. Fagi speciem unicam novi." The discrete capital letters appearing in his description refer to those line-drawings (on Table 351) of different organs of the common European beech. However, Tournefort failed to offer a specific epithet for this only Fagus species known to him.

To accommodate those plants with "aments" and a four-valved cupule which bears linear-like/thorn-like appendages, Tournefort established two genera: Fagus and Castanea, in 1700. (Castanea appeared on the same page, immediately following Fagus, with a good description, a table of line-drawings, and four specific epithets under a binomial system). In 1737, Linnaeus clearly and intentionally combined Tournefort's Fagus and Castanea as a single genus, Fagus; and offered a description of such a Fagus in his "Genera Plantarum" (p. 292). This description incorporates the diagnostic characteristics of these two kinds of plants. However, the distinction between them was indicated. Among the three Fagus species appearing in Linnaeus' "Species Plantarum" (1753: 997-998), two are Castanea (in Tournefort's sense) and one is Fagus (sylvatica, see above quotation). The generic concept and the description of such a Fagus were maintained in the fifth (1754) and sixth (1764) editions of Linnaeus' "Genera Plantarum".

Britton & Brown (1913: 614) designated F. sylvatica L. as the

type species of "Fagus (Tourn.) L. 1753", in their effort to typify all genera appearing in the second edition of their "Illustrated Flora of the Northern States and Canada". Farr et al. (1979: 665) regarded Britton & Brown's designation as lectotypification of "Fagus L. 1753", in their contribution to "Index Nominum Genericorum (Plantarum)".

Loudon commented on this matter in his influential book "Arboretum et Fruticetum Britannicum" (2 ed., 1854: 1949): "Linnaeus united the genus Castanea with Fagus, which was not done by any botanist before his time, and which has not been adopted by many of the moderns." I am not aware of any outstanding followers with regard to the Linnaean concept on the generic name Fagus. A consensus that Castanea should be regarded as a genus distinct from Fagus has been well established since the last century. Presently the name Castanea is consistently attributed to Miller, who published it in 1754. If Linnaeus had adopted Tournefort's concept of the generic name Fagus, it would be alright to cite "Fagus Tourn. ex L.", with reference to the Recommendation 46E.2 of the 1983 Code. Since it is Tournefort who first provided a description of Fagus with the generic concept adopted by us, in addition to the generic name itself, I feel it "useful and desirable" to cite the generic name as above.

Mirbel revised the circumscription of Tournefort's Fagus to accommodate species of Nothofagus recognized by him, in 1827. Such a concept of the generic name Fagus had been widely adopted in the last century, but abandoned in this century. This historical event is irrelevant to the citation of the generic name, thus there is no need to go further into this matter.

No segregates from the genus Fagus have been published up to this time.

2-3 A SYNOPTICAL KEY TO SUBGENERA AND SECTIONS

1A. Low-branching trees; normally with several major trunks. BARK
generally slightly yellowish; with larger and prominent lenticels.
CURRENT-YEAR-SHOOTS generally dark-colored and purplish/brownish;
thinner. BUDS clearly stipitate. LEAVES thin-chartaceous. LOWER
SURFACE of leaves glaucous. TERTIARIES generally clearly visible.
Primary/secondary POCKET-DOMATIA normally absent. MARGIN of leaves
slightly sinuous to slightly serrate. CUPULE-PEDUNCLE generally
glabrous; longer (5-7 cm), and more slender (generally no more than 1
mm); an angular dilated tip mostly present and conspicuous. NUT-
SCARS generally triangular/rounded. EAST ASIA.

Subgenus ENGLERIANA

1B. High-branching trees; normally with a straight and stout trunk. BARK
generally whitish/silvery; with smaller but still prominent
lenticels. CURRENT-YEAR-SHOOTS generally light-colored and
yellowish/brownish; thicker. BUDS normally sessile. LEAVES thick-
chartaceous. LOWER SURFACE of leaves concolored with the upper
surface (3 Sections) or glaucous (1 Section: Longipetiolata).
TERTIARIES generally obscure or even invisible. Primary/secondary
POCKET-DOMATIA always present. MARGIN of leaves crenate, slightly
sinuous, denticulate, or serrate. CUPULE-PEDUNCLE mostly at least

somewhat pubescent; shorter ((0.5)-1-3-(5)-((7)) cm), and stouter (generally no less than 1 mm thick); usually without an angular dilated tip). NUT-SCARS generally triangular. THROUGHOUT THE RANGE OF THE GENUS.

Subgenus FAGUS

2A.LOWER SURFACE of leaves glaucous; generally with short, unicellular hairs. PETIOLE generally $1/6-1/8$ as long as leaf-blade. CUPULE-PEDUNCLE (3)-4-6-(7) cm long. CUPULE-APPENDAGES linear. EAST ASIA (CHINA).

Section LONGIPETIOLATA

2B.LOWER SURFACE of leaves concolored with the upper surface; generally without hairs as described above (except in some taxa of Section Grandifolia). PETIOLE generally $(1/6)-1/8-1/12-(1/15)$ as long as leaf-blade. CUPULE-PEDUNCLE (0.5)-1-3-(5) cm long. CUPULE-APPENDAGES scale-like, or linear, or spatulate-foliaceous.

3A.SECONDARIES (12)-15-18-(20). MARGIN of leaves denticulate to sharply serrate, when denticulate generally with short, unicellular hairs on lower surface. SINUSES mostly concave, never convex. PETIOLE generally $(1/10)-1/12-1/15$ as long as leaf-blade. CUPULE-APPENDAGES linear. E NORTH AMERICA.

Section GRANDIFOLIA

3B.SECONDARIES (5)-8-12-(15). MARGIN of leaves crenate to slightly sinuous to slightly serrate, or denticulate to (slightly serrate); when slightly serrate, the teeth always restricted to the upper margin. SINUSES when present variously shaped, but

seldom concave. PETIOLE generally $(1/6)-1/8-1/10$ as long as leaf-blade. CUPULE-APPENDAGES scale-like or linear or spatulate-foliateous. EAST ASIA & WEST EURASIA.

4A. LOWER SURFACE of leaves and petiole (at least along midrib and secondaries) generally densely covered with long, unicellular hairs. MARGIN (crenulate) to slightly sinuous to slightly serrate, never denticulate. SINUSES when present concave. CUPULE-APPENDAGES linear, at least the basal ones somewhat spatulate-foliateous. WEST EURASIA.

Section FAGUS

4B. LOWER SURFACE of leaves and petiole at most sparsely covered with long, unicellular hairs. MARGIN denticulate to (slightly serrate) (Chinese plants), or crenate to slightly sinuous to slightly serrate (Japanese plants). SINUSES not concave (Chinese plants), or seldom concave (Japanese plants). CUPULE-APPENDAGES scale-like or linear (Chinese plants), or linear and with at least the basal ones somewhat spatulate-foliateous. EAST ASIA.

Section LUCIDA

CHAPTER 3

INFRAGENERIC TAXONOMIC TREATMENT

3-1 SUBGENUS ENGLERIANA CAMP EX SHEN

3-1-1 KEY AND DISCUSSION OF THE SUBGENUS

A diagnosis of the subgenus Engleriana has been offered in the synoptical key to subgenera and sections (see 2-3). A synoptical key to the species and subspecies recognized in this monograph is given as follows.

1A. LEAVES relatively small, 6-8 cm long; generally obovate to oblong.

APEX acute. **BASE** rounded. **SECONDARIES** (8)-10-12-(15). **MARGIN** slightly sinuous to entire; generally slightly recurved. **CUPULE-VALVES** with an acute apex; 8-10 mm long. **CUPULE-APPENDAGES** lanceolate, membranous; ca. 1.5-2.0 x 1 mm. **NUTS** level with or slightly exserted from the cupule-valves; always with very prominent wing along the entire length of each angle. **JAPAN**.

3-1-4 F. OKAMOTOI

1B. LEAVES larger, ((6))-(8)-10-12-(15) cm long; generally obovate to oblong/rhombic/elliptic to ovate. **APEX** acute-acuminate. **SECONDARIES** (12)-15-18-(20). **MARGIN** slightly sinuous to (slightly serrate/denticulate). The condition of the wing-like extension along

the nut-angles not as above.

2A.BARK with large, rhombic lenticels which are often broader than high. CUPULE-VALVES narrowly triangular, with an acute apex; (12)-15-20-(25) mm long. CUPULE-APPENDAGES linear, at least the upper ones with a spatulate-foliaceous tip. NUTS level with or slightly exserted the cupule-valves; with the wing-like extension only along the upper portion of each angle. CHINA & KOREA.

3-1-2 F. ENGLERIANA

2B.BARK with vertically elongated lenticels, which are sometimes further aligned in vertical lines or even connected with each other. CUPULE-VALVES narrowly triangular to suborbicular; (5)-8-10 mm long. CUPULE-APPENDAGES scale-like, narrowly triangular. NUTS exserted. The condition of the wing-like extension along the nut-angles generally not as above. JAPAN.

3-1-3 F. JAPONICA

3A.LEAVES narrower, long-elliptic to long-rhombic. CUPULE-VALVES narrowly triangular, with an acute apex; 8-10 mm long. CUPULE-APPENDAGES ca. 2 x 1 mm. NUTS with a discernible point-like projection along each angle. The exposed portion of the NUTS generally no more than 1/2 as long as the cupule-valves.

3-1-3b F. JAPONICA subsp. ANGUSTIFOLIA

3B.LEAVES broader, obovate to oblong/rhombic/elliptic to ovate. CUPULE-VALVES suborbicular to narrowly triangular; (5)-7-9-(10) mm long. CUPULE-APPENDAGES ca. 1.5-2.0 x 1 mm. NUTS generally without wing-like extension along the angles, but rarely with a

barely discernible wing along the upper portion of each angle.

The well exposed portion of the NUTS sometimes as long as the cupule-valves.

3-1-3a F. JAPONICA subsp. JAPONICA

The first published species of this subgenus is F. japonica, by Maximowicz in 1887. Three years later (1890), the Chinese plant now called F. engleriana was published as an apparent subvariety of F. silvatica var. longipes (= now F. longipetiolata) by Oliver, and provided with a description but no formal epithet. The name F. silvatica var. chinensis was validly published by Franchet in 1899, evidently referring to this plant. Franchet said that "Le F. silvatica var. chinensis rappelle surtout le F. japonica Maxim. par ses petites dimensions (of the leaves and fruits); mais, ..." (italics mine). Seemen published the first legitimate specific name F. engleriana for this plant in 1900; indicating that: "Nur F. japonica Maxim. kommt im Laube und den Frucht-Verhaeltnissen naeher heran an unsere Art; sie scheint mit ihr am meisten verwandt, obgleich in der Ausbildung der Cupular-Schuppen und dem Vorragen der Nuculae bedeutende Differenzen liegen." Based on years of field experience by Wilson in East Asia, Rehder & Wilson (1916: 191) first reported the similarity between F. japonica and F. engleriana in their bush-like branched tree-form. Noting also other similarities in leaves, they finally said that "The fruits are totally different, but these two species are undoubtedly closely related."

I fully agree with Seemen and Rehder & Wilson on the very close

relationship between F. japonica and F. engleriana. In addition, these two species are collectively well separated from all other species in numerous critical vegetative features, cupule-peduncle, and nut-scars (see 2-3). These differences collectively well segregate the genus into two subgroups. Camp had an infrageneric name "Englerianae" to stress the uniqueness of F. engleriana within the genus, in his unfinished manuscript (see Chapter 1). To memorialize the great effort made by Camp to comprehend the evolution and taxonomy of Fagus, I propose a subgenus, Engleriana Camp ex Shen, for these two species and a newly described local species, F. okamotoi. I see no need to further group species of this subgenus into sections.

3-1-2 FAGUS ENGLERIANA SEEMEN

Fagus engleriana Seemen, (1900 Sept.), Bot. Jahrb. 29: 285, Fig. 1, a-d.

[SYNTYPES: R.P. Farges s.n. (Sichuan-Chengkou), n.v.; A. Henry 6797, K (Color photo)!, E!, G!, GH!; B. von Rosthorn 1525, A!]

Fagus sylvatica L. var. longipes Oliver subvar. Oliver, ("bracteolis involucri exterioribus anguste spatulatim dilatatis"), (1890); in Hooker, J.D., Ic. Pl. 20: sub Pl. 1936. [COLLECTION CITED: A. Henry 6797]

Fagus sylvatica L. var. chinensis Franchet, (1899 July); J. Bot. (Morot) 13: 201. [HOLOTYPE: R.P. Farges s.n. (Sichuan-Chengkou)]

Fagus japonica sensu Nakai, non Maxim., (1917 Feb); Fl. Sylv. Kor. 3: 10-11, Pl. 1. [COLLECTION CITED: K. Okamoto (1916), Ulreung-Do; n.v.]

Fagus multinervis Nakai, (1918 May); Bot. Mag. (Tokyo) 32(377): 103-104.

[HOLOTYPE: K. Okamoto (1916)]

BUSH-LIKE TREES; normally branching from near the base to no higher than 2 m, generally with three to five major trunks; to 23 m tall, 60 cm DBH. **BARK** generally slightly yellowish, shiny, with the very smooth surface beset with large, rhombic lenticels which are often broader than high. **CURRENT-YEAR SHOOTS** generally dark-colored and purplish/brownish; glabrous. **BUDS** clearly stipitate even in July, the stipe 1-3 mm by the end of the growing season; slender-fusiform, the apex acute, ca. 15-20 x 3 mm. **BUD-SCALES** generally nearly glabrous along the upper margin. **LEAF-UNFOLDING** in middle to late April. **LEAVES** generally obovate to oblong/rhombic/elliptic to ovate to (lanceolate); ((6))-8-12-((15)) cm long; thin-chartaceous. **APEX** (acute) to acuminate. **BASE** cuneate to rounded; often prominently unequal. **UPPER SURFACE** dark green. **LOWER SURFACE** glaucous; rarely with long, whitish/yellowish, unicellular, silky hairs persistent on the midrib and secondaries. **SECONDARIES** (12)-15-18-(20); generally abruptly curving upward when closely approaching the margin. Primary/secondary **POCKET-DOMATIA** normally absent. **MARGIN** slightly sinuous to (slightly serrate/slightly denticulate). **PETIOLE** generally 1/8-1/12 as long as the leaf-blade.

Flowers per **MALE-INFLORESCENCE** ca. 15-31. Hairs on the upper portion of the **PERIANTH-TUBE** eglandular or glandular (then black). **ANTHERS** reddish. **FRUIT MATURING** in middle to late July. **CUPULE-PEDUNCLE** ca. 5-7 cm long, no more than 1 mm thick; generally glabrous; an angular dilated tip always present and conspicuous; pendulous when

the fruits mature. CUPULE-VALVES narrowly triangular, the apex acute; (12)-15-20-(25) cm long; thin. CUPULE-APPENDAGES linear, at least the basal ones (sometimes all of the cupule-appendages) with a discernible spatulate-foliaceous tip (sometimes the whole cupule-appendages broadly spatulate, dark green, resembling a normal leaf). NUTS level with or slightly exserted from the cupule-valves. The wing-like extension along the nut-angle always present, but confined to the upper portion of each angle, varying from point-like to wing-like. NUT-SCARS generally triangular/rounded. CHINA & KOREA.

LECTOTYPE: A. Henry 6797, CHINA, Hubei-Fang. K! (in color-photo form, the specimen housed in K not seen)

ISO-LECTOTYPES: E!, G!, GH!. Lectotypified by Chang & Huang, (1988), Acta Phytotax. Sin. 26: 114.

Seemen cited three collections in the description, but did not designate a type. Among the three collections, I have only seen A. Henry 6797 and P. Bork & A. von Rosthorn 1525. The former is a beautiful collection, exhibiting rather typical appearance of the species, and has duplicates housed in several major herbaria. The statement made by Chang & Huang (1988: 114) under Fagus engleriana that "The type specimen was collected from Sichuan, Chengkou: A. Henry 6797." (my translation from Chinese), is here considered as a lectotypification of the species, though the locality was confused.

The specific epithet was proposed to commemorate Adolf Engler.

ILLUSTRATIONS:

Seemen (1900: Fig. 4, a-d); Nakai (1917: Pl. 1); Chang (1966: Pl. 17); Anonymous (1972: p. 408); etc.

DISTRIBUTION AND ECOLOGY:

F. engleriana has a disjunct distribution in SE China and a small island (ca. 73 square km) in the Sea of Japan (= East Sea of Korea). The latter, Ulreung-Do (Kyonbuk Prov.), is 135 km off the eastern coast of the Korean Peninsula. In China, the species is also disjunct in two areas. Within its far larger western range (Sichuan, Gueizhou, and W Hubei; ca. 25-34 degrees N), it is found in montane regions higher than 1,200 m; it does particularly well at elevations of 1,800 to 2,500 m. Within its eastern range (S Anhwei and NW Zhejiang; ca. 29.5-30.5 degrees N), it appears from 900 to 1,700 m alt. In Ulreung-Do (ca. 37.5 degrees N), it abounds from ca. 300-900 m, and forms nearly pure forest on the northern slope. For distribution maps, see Tsien et al. (1975: 11) and Chang (1981: 49).

Along the eastern portion of Dabashan Range, which demarcates the different climatic and ecological belts of central and eastern China, F. engleriana grows with F. hayatae ssp. pashanica, F. lucida, F. brevipetiolata, and some other trees in various associations. This is the only region within the current range of the genus Fagus where one can easily find three good beech species growing in the same stand. Among the four well known Chinese beech species (F. longipetiolata, F. lucida, F. hayatae, and F. engleriana), this species extends the farthest north (well beyond the northern slope of Dabashan Range, in S Shaanxi, ca. 35.5 degrees N). When sympatric with other species, it

normally grows at or extends to higher elevations (except in the NE Sichuan portion of the Dabashan Range, where it grows with F. hayatae ssp. pashanica). The ecology of F. engleriana is further discussed in 3-1-3.

TAXONOMIC REMARKS:

The leaves of F. engleriana are so similar to those of F. japonica that if there were no significant differences in other critical respects, specimens under these two names could be lumped together under the same specific epithet without a need of further division. Some of those trivial differences are well-overlapping quantitative ones. Others might disappear when more specimens, both fertile and sterile ones, are available for comparison. However, these two species are sharply different in features of the cupules and nuts, and the nature of the lenticels on the bark, in addition to their discrete distribution range. It is the introduction of the Korean plants that causes a taxonomic problems.

Nakai identified a sterile specimen from Ulreung-Do of Korea as F. japonica in 1917, but later (in 1918) he considered it to represent a new species F. multinervis Nakai. Study of the fruiting materials has convinced most later authors that the Korean plants are essentially similar to the Chinese F. engleriana (see Ohkubo et al., 1988; and the references cited therein). Kurata (1964: 88) considered F. longipetiolata, F. engleriana, and F. multinervis to be closely allied to F. japonica. Y.-N. Lee (1967) consigned F. multinervis to synonymy under F. japonica, based on similarities on leaves, anthers, and pollen

grains. T.-B. Lee (1985) reduced the Korean plants to a variety of F. crenata, in his "Illustrated Flora of Korea".

At my disposal there are about 40 fertile collections of F. engleriana from its whole range in China (counting each of the two population samples as a single collection), and four fertile collections from Ulreung-Do. On the basis of these materials, it is clear that the Korean specimens are not at all differentiable from the Chinese ones identified as F. engleriana. The Chinese plants and the Korean plants are further similar in having more numerous major trunks than F. japonica (see Yim et al. 1980; Kim et al., 1986). The features that Y.-N. Lee used to associate "F. multinervis" with F. japonica are not pertinent, because the Korean plants are just as similar to F. engleriana as they are to F. japonica based on these same features.

Ulreung-Do is over 1,000 km northeast of the northeasternmost locality (Anhui-Huangshan) of F. engleriana in China. The history of the beech forest in Ulreung-Do is unknown. This small volcanic island is elevated ca. 1,000 m above the sea of about 2,000 m depth. This volcano first arose during the Miocene (for a concise geological history of Ulreung-Do, see Yim et al., 1980; Kim et al., 1986; among others). It seems obvious that the history of the current populations of F. engleriana in Ulreung-Do will not be older than the current interglacial, based on the geological and climatic histories of the general region of Ulreung-Do. Therefore, long-distance dispersal, either by birds or by wind, will be the most likely way for the initial establishment of F. engleriana there.

No infraspecific names have been proposed for F. engleriana. A

reasonable degree of variation in many features which are observable on specimens, is present throughout the range. Some level of regional differentiation at or higher than the population level is observed. Nevertheless, within the range of F. engleriana in China, I fail to detect any appreciable and consistent infraspecific covariation patterns to allow me to establish subspecific taxa. The only fruiting collection which does not show conspicuous foliaceous cupule-appendages is from the eastern range (Zhejiang-Anji). It is further peculiar in its very prominently winged nuts. Otherwise this specimen does not look strange to me. These two traits, though rare, are not outrageous for the species to which this specimen belongs. They are better considered as quantitative variants of the corresponding features of F. engleriana. Unless more collections showing similar traits come to hand, I am reluctant to give this specimen an infraspecific name. As expressed above, the variation range of critical features shown by the Korean plants falls well within that shown by the Chinese plants.

3-1-3 FAGUS JAPONICA MAXIM.

Fagus japonica Maxim., (1887), Bull. Acad. Imp. Sci. St. Petersb. 31:

101. [HOLOTYPE: Tschonoski (1864), LE, n.v.; ISOTYPES: A!, G!, GH!,
US-39343 !]

Fagus japonica Maxim. subsp. angustifolia Shen, subsp. nov.

BUSH-LIKE TREES; normally branching at a position generally no higher than 2 m, generally with two to four major trunks; to 30 m tall, 1 m DBH. **BARK** generally slightly yellowish, shiny; the very smooth surface with vertically elongated lenticels, which are sometimes further aligned in vertical lines or even connected with each other. **CURRENT-YEAR-SHOOTS** generally dark-colored and purplish/brownish; glabrous. **BUDS** clearly stipitate even in July, the stipe 1-3 mm long by the end of the growing-season; slender-fusiform, the apex acute, ca. 15-20 x 3 mm. **BUD-SCALES** generally nearly glabrous along the upper margin. **LEAF-UNFOLDING** in middle to late April. **LEAVES** generally obovate to blong/rhombic/elliptic to ovate to (lanceolate); ((6))-10-12-(15) cm long; thin-chartaceous. **APEX** (acute) to acuminate. **BASE** cuneate to rounded; often prominently unequal. **UPPER SURFACE** dark green. **LOWER SURFACE** glaucous; often covered with long, whitish, unicellular, silky hairs, at least along the midrib and secondaries. **SECONDARIES** (12)-15-18-(20); generally abruptly curving upward when closely approaching the margin. Primary/secondary **POCKET-DOMATIA** normally absent. **MARGIN** (crenate) to slightly sinuous to (slightly serrate/slightly denticulate). **PETIOLE** generally 1/8-1/12 as long as the leaf-blade.

Flowers per **MALE-INFLORESCENCE** ca. 15-31. Hairs on the upper portion of the **PERIANTH-TUBE** normally glandular (then black). **ANTHERS** reddish. **FRUIT MATURING** in middle to late July. **CUPULE-PEDUNCLE** ca. 5-7 cm long; no more than 1 mm thick; generally glabrous; an abruptly dilated tip almost always present, but sometimes not very conspicuous; mostly pendulous when the fruits mature. **CUPULE-VALVES** narrowly triangular to suborbicular, (6)-8-10 mm long; thin. **CUPULE-APPENDAGES**

scale-like, narrowly triangular; ca. 1.5-2.0 x 1 mm. NUTS normally exserted; with or without a narrow wing-like extension along each angle. NUT-SCARS generally triangular/rounded. JAPAN. Two subspecies recognized.

HOLOTYPE OF SUBSP. JAPONICA:

Tschonoski (1864), JAPAN, Honshu-Kanagawa; LE, n.v.; ISOTYPES: A!, G!, GH!, US-39493 !

HOLOTYPE OF SUBSP. ANGUSTIFOLIA:

D. Michener & E. Bennett 1974, JAPAN, cult. in A (AA-23182-A); A!

This subspecies is based on two trees cultivated in the Arnold Arboretum, Boston, Massachusetts, U.S.A.. Both are mature trees and higher than 15 m. They are of different origin. The tree with the accession number AA-23182-A is here designated as the **type-tree**. This individual, whether procured as a seed or as a sapling, is clearly of Japanese origin. No further information about its origin is available.

ILLUSTRATIONS:

Subsp. japonica: Kurata (1964: Pl. 44); Hayashi (1969: 198); Ohba (1989: Pl. 79); etc.

Subsp. angustifolia: None.

DISTRIBUTION AND ECOLOGY:

The distribution and ecology of subsp. angustifolia are almost unknown. However, the general ecological characterization of the subsp.

angustifolia will not significantly differ from that of subsp. japonica under the following two considerations. First, both the geographical distribution and the ecological amplitude of F. japonica are not large for a cold-deciduous hardwood tree species. Second, no significant ecological differences have been detected between infraspecific taxa for species and subspecies of Fagus that are comparable with F. japonica in the area of distribution and amplitude of ecological adaptation.

Fagus japonica grows in almost all prefectures of Honshu, Shikoku, and Kyushu, - three of the four major islands comprising Japan. It is absent at least in Aomori, Yamagata, Niigata, Ishikawa, Saga, Nagasaki, and Kagoshima (listed from north to south; all along the Japan-Sea). Japanese botanists seemingly have no trouble in identifying sterile specimens of F. japonica and F. crenata, to my knowledge. [For a good contrast on vegetative features between them, see Hayashi (1969: 197)]. The dotted distribution maps of F. japonica published by Kurata (1964), and Hayashi (1969: 198) are very similar. It is well known that F. japonica is basically a species of the "Outer Zone of Japan". In its northern range, it is chiefly distributed along the Pacific Ocean-side of the Japanese Archipelago, where the central divide is high enough to cause different climatic regimes in the "Outer Zone of Japan" and "Inner Zone of Japan". The central divide, Ou Range, retains most of the moisture carried by the monsoon from the Pacific Ocean in summer, while checking the Mongolian High Pressure in winter. Along with the warm ocean-current, Kuroshio, this results in a more rainy summer and a warmer whole-year climate in the Outer Zone of Japan. As to the southern range of F. japonica, roughly south of 35 degrees N, the

climatic differentiation along each aerial latitudinal profile becomes trivial, at least in terms of the growth of cold-deciduous trees.

It is necessary to mention F. crenata when the distribution and ecology of F. japonica are to be discussed. Both the geographic range and ecological amplitude of F. crenata are larger than those of F. japonica. These two species overlap in both respects. In almost the entire range of F. japonica, F. crenata is also present. (For distribution maps of F. crenata, see Anonymous (1949: 61), Kurata (1964), and Hayashi (1969: 196).) When they are sympatric (in montane regions), F. japonica usually grows at lower elevations than F. crenata. They are often found in the same mixed deciduous hardwood stand. In these cases, F. japonica tends to be better represented on the steeper slopes, while F. crenata has more individuals on more moderate slopes and level ground.

Like the closely related F. engleriana, F. japonica is a mountain-inhabitant. The populations are concentrated in the low-montane regions of Honshu; ca. 300 m in the north and ca. 1,300 m in the south. It descends to about 100 m alt. at its northern limit in Honshu. Its occurrence at ca. 1,800 m in Honshu sharply contrasts to its altitudinal range in Shikoku and Kyushu (ca. 700-1,100 m), which are more southern and have mountains ca. 1,800 m high.

It may be proper to begin the discussion of the bioclimatic adaptation of beech species with F. japonica, because its geographic range is neither very large nor very small, and because a considerable amount of information is available concerning this species. In Honshu, F. japonica is an important element of the so-called "Castanea zone"

(see Hara, 1959). This is a floristic zone, widely used in Japanese vegetational literature because of its accepted ecological connotation. According to Hara (1959: 44-45), the Castanea zone is a vertical montane zone from ca. 600-700 m to 1,200-1,300 m alt. in the central Honshu mountains. In their excellent work on the vegetation zones of Japan and adjacent regions, Hamet-Ahti et al. (1974: 70-74) attributed this zone and its equivalents to the "hemitemperate subzone". Their categorization of the bioclimatical zones is extremely detailed. (They have four subzones within each major zone: Meridional (Warm temperate-Subtropical), Temperate, Boreal, and Arctic. The montane equivalents of these four major zones have a prefix "oro". The four subzones are denoted by the subheadings: hemi, southern, middle, and northern.) Based on their discussion about the hemitemperate subzone in Japan, it is clear that the entire distribution of F. japonica, both horizontal and altitudinal, coincides very well with the hemitemperate subzone, with only two minor exceptions. First, F. japonica is not present in some localities within the western territory of the hemitemperate subzone, because of the "Outer Zone of Japan" nature of the species. Second, F. japonica can ascend to ca. 1,800 m alt. in Honshu, which is explainable by the local adaptation of some populations.

Based on physiognomy and another set of major climatic parameters, Wolfe (1979: 13) treated Hara's Castanea zone as a synonym of his re-defined "Mixed Mesophytic Forest". The Mixed Mesophytic Forest, as defined by Wang in 1961, embraces nearly all of the so-called relic elements of the Tertiary mixed coniferous/deciduous hardwood forest which had occupied vast land areas in the Northern Hemisphere

before the climatic deterioration. In addition, some "temperate" families (or the "temperate" members of them) such as Aceraceae, Betulaceae, Fagaceae, Juglandaceae, etc., show their greatest diversity in this vegetation unit.

Equipped with the rather clear ecological characterization of F. japonica at least in terms of its vegetational attributes, I can look into the situation of F. engleriana in China. According to the nationwide climatic classification, as cited in Wu (1980: 30-33), four major zones are recognized: Tropical, Subtropical, Temperate, and Cool temperate. The Subtropical zone is subdivided into southern, middle, and northern subzones; and the Temperate zone has two subzones: warm temperate and temperate. Because of the different climatic criteria applied, the degree of detail and the purpose, it is difficult to compare the Chinese system with that proposed by Hamet-Ahti et al. (1974). Nevertheless, some preliminary identifications and equations can be presented here. First, the hemitemperate subzone of Hamet-Ahti et al. (1974) is missing from the Chinese system. [This subzone was considered as a transitional belt between the Meridional (= Subtropical, in most common usage, judging from the context) zone and the Temperate zone by them.] Second, this missing belt should be inserted between the Subtropical zone and the Temperate zone in the Chinese system. Third, this belt may be characterized by a mean annual temperature of ca. (9)-10-12-(13) degrees C, a mean warmest month temperature of ca. (20)-21-25-(27) degrees C, and a mean coldest month temperature of ca. 0-minus 2 degrees C. (see Wolfe, 1979: Pl. 2). Fourth, such a temperature regime is not currently available in lowlands of at least the Northern

Hemisphere. On lowlands, as a rule, the rate of decrease of winter temperature is generally greater than that of summer temperature with the increase in latitude. The summer temperature of this belt is similar to that of the warmer part of the temperate regions, but its winter temperature is somewhere around those of cooler subtropical regions and warmer temperate regions. Fifth, this interpretation can explain why F. japonica and some other beech species are exclusively mountain-inhabitants. For F. engleriana, more discussion is necessary.

In China, F. engleriana also occurs in the Mixed Mesophytic Forest vegetation, but its populations are not centered there. Higher than that there is a "Mixed Deciduous Broad-leaved Forest" (see Wolfe, 1979: 14-15). Fagus engleriana is an important element of this vegetation in China, as are also F. lucida and F. hayatae ssp. pashanica. Moreover, it often forms pure or nearly pure stands below the coniferous forest belt, which mostly has Picea species as the major components. It even sometimes forms the timberline, as in its eastern range. In Ulreung-Do, F. engleriana abounds from ca. 300 m to ca. 900 m alt. It forms nearly pure forests on the north slope of that volcanic island. In the map prepared by Hamet-Ahti et al. (1974: 67), Ulreung-Do is situated in the northern part of their hemitemperate subzone. However, at least two basic points set the montane vegetation of Ulreung-Do well off the Mixed Mesophytic Forest (sensu Wolfe, 1979), but place it very close to Wolfe's Mixed Northern Hardwood Forest (p. 16-17): first, the too low winter temperature; second, the nearly overwhelming predominance of a deciduous species. Thus, there seem to be no significant ecological differences between the Chinese populations

and the Korean one of F. engleriana. As a conclusion, it is clear that F. japonica and F. engleriana show essentially different adaptation to temperature.

TAXONOMIC REMARKS:

Only 13 fruiting collections of F. japonica are available for my research. Among them, three (actually three cultivated trees in the Arnold Arboretum, two of them genetically identical) are segregated into a subspecies (angustifolia). Nevertheless, the variation shown by the remaining collections is rather large. The type collection has small leaves with fewer secondary veins, suborbicular cupule-valves, and two equally developed nuts which sometimes have a recognizable protrusion on the upper portion of their angles. The cupule shape of the type collection is "normal" for F. japonica, but at least the other two points need some comments.

As is widely known, leaves on the fertile shoots of many deciduous hardwoods tend to be smaller than those on sterile ones. This is not surprising when the differences between sun and shade leaves on the same tree are considered. Reproductive shoots of beeches are developed around the crown and other exposed portion of the tree. The small leaves of the type collection at least in themselves should not be considered as taxonomically important. As to the fewer secondary veins, another observation is pertinent. That is, at least within a subspecies of any beech species, it is almost a rule that the number of the secondary veins is positively correlated with the size of that leaf.

The nuts of F. japonica are "normally" without any recognizable

extensions along their angles, according to literature and my limited observation on those specimens at my disposal. However, the wing-like extensions along the upper portion of nut-angles are more or less discernible on a few specimens.

The very narrowly triangular cupule-valves are considered as a characteristic of the subspecies angustifolia. This trait is however observed on a few specimens of the typical subspecies. Another two features that vary significantly within the species are the number of nuts per cupule and their relative size. Camp has illustrated a cupule that contains three equally developed large nuts. On a specimen from the type tree of the subspecies angustifolia (D. Michener & E. Bennett 1974, A), a 6-valved cupule is present along with 4-valved cupules. On a specimen from another individual of the same subspecies (AA-14587-B, P.S. Green (1964-10-8), A), an 8-valved cupule is present along with 4-valved cupules. Hayashi (1969: 199) has a variety pleiosperma, based on a few individuals found in one locality. They usually have three to five nuts contained in cupules with normally more than six cupule-valves. Cupules with more than four cupule-valves and then containing more than two nuts have been reported and illustrated for F. sylvatica (Hjelmqvist, 1948: 85). They have also been reported for F. grandifolia (in the United States) and F. engleriana (Chang, 1966: 117). I have observed them on a specimen of the Mexican beech. They are evidently extremely rare in any species, if present at all, except in F. japonica. Particularly interesting with F. japonica is that when extra nuts are present they are sometimes equally well developed and flanked by equally well developed cupule-valves. This condition has not been found in any

other species in my knowledge. In other words, in some cases the multi-nutted cupules of F. japonica have a "normal" configuration and were developed through a "normal" ontogeny. This sharply contrasts the seemingly teratological development of the multi-nutted cupules observed on other species.

Sometimes the nuts in the same cupule vary in size. This is evident on three among the 13 collections at my disposal. Camp has illustrated one cupule of this sort. The difference in size in most of these cases is prominent. I have observed size variation between the two nuts in the same cupule on F. lucida. Although the degree of the difference in size in F. lucida is obviously smaller than that in F. japonica, it is clear that this sort of variation is associated with the evolutionary reduction of the entire cupule/nut complex in both species. Camp has illustrated a single-nutted cupule of F. japonica. There is no reason to assume that the cupule of that nut is four-valved. Such a cupule/nut complex is highly comparable with those "normally" occurring in F. lucida.

According to Kurata (1964: 88), local people can distinguish up to eight variants of F. japonica, based on differences in ecology, wood features, and bark features. Some of them are sympatric in some localities. Kurata has suggested these interesting variations to be the subject of future research. Unfortunately, I have had no chance to examine the type collection of Hayashi's variety. The only segregation I can make is the subspecies angustifolia, based on the limited fruiting specimens at my disposal. Its generally narrower leaves, with the shape ranging from rhombic to elliptic, are not seen in any other specimen

under my study, including sterile ones, which are about forty in number. It is further peculiar in its lanceolate and spreading cupule-appendages. Lanceolate appendages are also observed in the typical subspecies, though rare. In those cases they are appressed on the surface of the cupules, as the "normal" triangular ones. Though all three individuals here assigned to the subspecies angustifolia are cultivated, it seems unlikely that their peculiar traits were developed under some kind of environmental stimulus which is not present or working on the populations of subsp. japonica in Japan.

3-1-4 FAGUS OKAMOTOI SHEN, SP. NOV.

DECIDUOUS TREES. CURRENT-YEAR SHOOTS generally dark-colored and purplish/brownish; glabrous. BUDS clearly stipitate even in July, the stipe 1-3 mm by the end of the growing season; slender-fusiform, the apex acute. BUD-SCALES generally nearly glabrous along the upper margin. LEAVES generally obovate/oblong; 6-8 cm long; thin-chartaceous. APEX acute. BASE (cuneate) to rounded. UPPER SURFACE dark green. LOWER SURFACE glaucous; sometimes covered with long, whitish, unicellular, silky hairs along the midrib and secondaries. SECONDARIES (8)-10-12-(15); generally abruptly upcurved close to the margin. Primary/secondary POCKET-DOMATIA absent. MARGIN slightly sinuous to entire; generally slightly recurved. PETIOLE generally 1/8-1/12 as long as the leaf-blade.

FRUIT MATURING in early to middle July. CUPULE-PEDUNCLE ca. 5-7

cm long; no more than 1 mm thick; glabrous; an angular dilated tip sometimes present, but never very conspicuous; mostly pendulous when the fruits mature. **CUPULE-VALVES** narrowly triangular; ca. 6-8 mm long; thin. **CUPULE-APPENDAGES** lanceolate; foliaceous and membranous; ca. 2 x 0.6-0.8 mm. **NUTS** level with or slightly exserted from the cupule-valves; always with very prominent wing along the entire length of each angle; with the lower portion blackish. **JAPAN.**

Based on four fruiting collections.

HOLOTYPE:

S. Noshiro 1606, JAPAN, Honshu-Yamanashi; TUS-75454 !

The specific epithet is to honor OKAMOTO Motoharu of the Osaka Museum of Natural History, Osaka, Japan. His excellent works in exploring new and interesting features useful in the taxonomy of Fagaceae, and those on the ontogeny of the cupule of Lithocarpus are highly regarded.

ILLUSTRATIONS:

None.

DISTRIBUTION AND ECOLOGY:

Only four fruiting collections (and specimens) are assigned to this new species. They are from three different localities: Tochigi (two collections), Tokyo (one), and Yamanashi (one), from north to south. The line connecting them is nearly straight, in a north-south trend, and no longer than 200 km. One of the two from Tochigi was

collected along the Chuzenji Lake at about 1,300 m altitude. Another Tochigi collection was from the same general region. Many specimens of F. japonica at my disposal are from there. The collection from Tokyo was made in Takao Mt., where F. japonica abounds. The type collection was from a location of an elevation of 1,420 m. However, it still seems possible that the populations of this species are concentrated within an altitudinal range higher than that most suitable for F. japonica.

TAXONOMIC REMARKS:

Though the geographical range of F. okamotoi is well within that of F. japonica, the two species are well separated by the features of the cupule/nut complex. The cupule-appendages of F. okamotoi are membranous, drying brownish, commonly with the very tip narrowly acute; while those of F. japonica are basically scale-like, thick, drying whitish, with the very tip roundish. The elongate appendages found in a few specimens of F. japonica may approach those of F. engleriana in their roundish/flattened cross-sectional shape and the whitish color when dried. The nuts of F. okamotoi always have broad wings along the entire length of the angles. Neither F. japonica nor F. engleriana shows this trait.

Another feature about the shape of the beechnuts should be mentioned in this connection. Almost as a rule, the degree of plumpness of a nut is negatively correlated with the degree of the development of the wing, regardless of its taxonomic identity. The nuts of F. japonica are regularly plump, with the cross-sectional shape conforming to a geometric triangle; those of F. engleriana are mostly but not always

similar; but those of F. okamotoi are very "shrunkened". In a "shrunkened", cross-sectionally very concave beechnut, one cannot expect a reasonably well developed seed, in my experience. However, I fail to detect appreciable difference in the rate of good seeds and/or rate of germination from the silvicultural literature of the species "normally" producing wingless and plump nuts (such as F. japonica) and those "normally" producing at least somewhat winged and "shrunkened" nuts (such as F. crenata, F. grandifolia and F. sylvatica).

If the general appearance of the trigonobalanoid cupule/nut complex is taken as most similar to the ancestral condition of the whole family, that of F. japonica may be considered as closest to the ancestral condition of the genus Fagus, based on the associated discussions presented in this section. Among these ancestral expressions, the occasional "seemingly normal" multi-nutted cupules, very small and very thin cupule-valves, scale-like and horizontally aligned appendages, and the plump and unwinged nuts, are particularly outstanding. However, the very long and slender cupule-peduncle and the rounded/triangular nut-scars should be considered as autapomorphic for the subgenus. F. engleriana has highly derived appendages, and a rudimentary development of the wing-like extension only on the upper portion of the nut-angles. A rudimentary development of the F. engleriana-type appendages and a similar (to F. engleriana) degree of development of wing-like extensions on nuts are observable on at least subspecies angustifolia of F. japonica. Even the narrowly elliptic/oblong leaves of this subspecies are present in F. engleriana; they are not seen in the typical subspecies, as mentioned already.

Based on eight collections, Chang (1966: 117) said that "All specimens from Huangshan (of Anhuei) have smaller leaves and cupules, the latter without green and foliaceous appendages." (translation and italics mine). Two of those eight collections are available to me. They do have smaller leaves and cupules, as does the only additional fruiting collection from the eastern range of the species (Zhejiang-Anji) at my disposal. However, it is this Zhejiang specimen that does not have conspicuous foliaceous appendages (see 3-1-2), among these three.

There are at least two reasons to retain the entity angustifolia within F. japonica. First, the available information about this taxon is hardly more than that allows me to establish it. Second, judging from the available information, the degree of continuity in the critical taxonomic features is obviously stronger between this subspecies and the typical subspecies based on Tschonoski (1864) than between it and F. engleriana.

The situation of F. okamotoi in this regard is quite different. After I found that the cupule/nut complex of some fruiting specimens identified (as received) as F. japonica is different from that of the type collection of F. japonica, I immediately saw the difference between them in leaves. Fagus okamotoi has smaller and obovately oblong leaves which mostly have a rounded base. Leaves of this nature are observable on some specimens of F. japonica subsp. japonica, but they are only present on the distal portion of shoots. In other words, they cannot be considered as useful for taxonomical characterization of F. japonica because they are poorly developed leaves due to physiological constraints. The cupule-appendages and the nuts of F. okamotoi are

highly different from those of both F. engleriana and F. japonica, and collectively represent another direction of evolution of the cupule/nut complex. Associated with its distinct leaves, this well marks another species unknown to science previously, and reveals another evolutionary pattern within the subgenus.

3-2 SUBGENUS FAGUS

A diagnosis of the subgenus *Fagus* and those of the four sections have been offered in the synoptical key to subgenera and sections (see 2-3). A synoptical key to the species and subspecies within each section will be given under that particular section.

Two members of this subgenus have shaped the rather stereotyped impression about the general external features of beeches in the mind of Euro-American botanists and the general public: F. sylvatica and F. grandifolia. Though they are very different in their leaves, the general similarity in the cupule/nut complex between the beeches growing in the New England region and those common in western Europe is evident. This really makes sense in the general definition of this subgenus. The geographic range of this subgenus is just the range of the entire genus. The disjunct distribution of the genus reflects the disjunct distribution of this subgenus. The amplitude of environmental adaptation of this subgenus, as exhibited by its members, is also broader than that of the other subgenus, *Engleriana*.

The trans-Northern-Hemispheric distribution of this subgenus in

the Tertiary is supported by two points. First, almost no fossil beeches found outside East Asia could be convincingly assigned to the subgenus Engleriana. (However, the case of F. altaensis in Central Asia is arguable.) Second, on the other hand, almost all beech fossils found outside East Asia could be explained at least theoretically as members of the subgenus Fagus.

Although many critical taxonomic features vary significantly within the subgenus Fagus as defined here, members of this subgenus show many shared expressions that are not present in the subgenus Engleriana. Some of them are clearly plesiomorphic for the whole genus, such as the high-branching tree-form, sessile buds, thick-chartaceous leaves, short and stout cupule-peduncle, triangular nut-scars, etc.; while the remaining are autapomorphies for the subgenus, such as the well developed pocket-domatia, reduction of the subtending bracts of the cupule, thick cupule-valves, linear and hairy cupule-appendages, etc. The subgenus Engleriana shows contrasting character-states with the subgenus Fagus in all of the features enumerated above. In other words, within the subgenus Engleriana, all features appearing in the former group are expressed as autapomorphies; while most (three out of four) features listed in the latter category are present as plesiomorphies (the last feature has evolved within the subgenus into two autapomorphies in two species). The subgenus Engleriana is far more uniform in leaf features, compared with the subgenus Fagus. Nevertheless, the latter shows an infra-subgeneric evolutionary trend which is not seen in the former, that is, the occurrence of the short, warty, unicellular hairs on the lower surface of leaf-blade (in sections

Longipetiolata and Grandifolia).

After these discussions and comparisons, I would like to advance the following statements. First, these two entities are in themselves well defined morphologically. Second, they are nearly equal in terms of weight after counterbalancing through various arguments as presented above. Third, within each subgenus, the relative degree and speeds of diversification between vegetative (chiefly leaves) and reproductive (chiefly cupules) features differ. Within the subgenus Engleriana, cupule evolution is more prominent than leaf evolution; within the subgenus Fagus, leaf evolution is more outstanding than cupule evolution. Fourth, for the subgenus Engleriana, the first appearance of its characteristic leaves could have marked the evolutionary establishment of the subgenus. Fifth, for the subgenus Fagus, I cannot find any unifying and sharply distinct characteristics that can mark the point of origin of the subgenus. The autapomorphies of this subgenus, as mentioned before, are either developed after the evolutionary debut of the subgenus (linear and hairy cupule-appendages, and the reduction of the subtending bracts of cupules), or developed through parallelism (pocket-domatia), or not very important (thick cupule-valves). Sixth, the lack of handsome autapomorphies of the subgenus Fagus and a bunch of beautiful autapomorphies of the subgenus Engleriana altogether indicate that: the differentiation between them reflects an unequal branching caused by the rapid evolution in the ancestry of the subgenus Engleriana. Seventh, at least because of this, the subgenus Fagus can be regarded as representing the "mainstream" of the evolution of the genus Fagus. Eighth, the evolution of these two subgenera (after this

"branching") reveals different patterns. For the smaller subgenus Engleriana, the evolutionary modification of cupule/nut complex is amazing. For the much larger subgenus Fagus, the amplitude of evolution of cupule/nut complex is not significantly broader than that of the subgenus Engleriana, but its leaves evolved tremendously. Finally, these two entities are genetically sharply differentiated.

Again, I do not see any convincing selective advantage for the several apomorphies discussed above, in contrast to the corresponding plesiomorphies. The apomorphies might reflect random fixation of genetic novelties that were initiated as random mutations in individual taxa or as parallel mutations in sibling taxa (reflecting their similar genetic potential). To close this section, I simply cannot find an alternative explanation of the first-level infrageneric division.

3-3 SECTIONS OF THE SUBGENUS FAGUS: SECTION LONGIPETIOLATA SHEN, SECT. NOV.

3-3-1 KEY AND DISCUSSIONS OF THE SECTION

A diagnosis of this section within the subgenus has been offered in the synoptical key to subgenera and sections (see 2-3). Two synoptical keys to the species of this section are given as follows.

SYNOPTICAL KEY BASED ON VEGETATIVE FEATURES:

1A.CURRENT-YEAR SHOOT relatively slender, ca. 1 mm thick; light-colored, yellowish/brownish. **LEAVES** thin-chartaceous.

2A.LOWER LEAF-SURFACE without glandular hairs (unique in the section).

BUDS slender-fusiform; with an acute apex. **LEAVES** narrowly ovate-lanceolate. **APEX** acuminate to caudate. **BASE** rounded to broadly cuneate. **PETIOLE** shorter, ca. 1/10-1/12 as long as the leaf-blade.

3-3-3 F. BREVIPETIOLATA

2B.LOWER LEAF-SURFACE with glandular hairs. **BUDS** slender-fusiform or narrowly ovoid; with an acute or blunt apex. **LEAVES** ovate-elliptic. **APEX** acuminate. **BASE** rounded to cuneate. **PETIOLE** longer, ca. 1/8-1/9 as long as the leaf-blade.

3-3-5 F. TIENTAIENSIS

1B.CURRENT-YEAR SHOOT stouter, more than 1 mm thick; generally dark-colored and purplish/brownish. **LEAVES** thick-chartaceous. **BUDS** ovoid; with a blunt apex. **PETIOLE** long, ca. 1/6-1/8 as long as the leaf-blade.

3A.LEAVES (narrowly ovate) to ovate/trullate to oblong to (elliptic)).

APEX acuminate to (acute). **BASE** broadly cuneate to narrowly cuneate to concave. **MARGIN** (slightly crenate)-slightly denticulate-slightly serrate.

3-3-2 F. LONGIPETIOLATA

3B.LEAVES generally ovate. **APEX** acute. **BASE** cuneate. **MARGIN** compound-serrate.

3-3-4 F. BIJIENSIS

SYNOPTICAL KEY BASED ON REPRODUCTIVE FEATURES:

1A. CUPULE-PEDUNCLE relatively slender, generally somewhat less than 1 mm thick; ca. 2-3 cm long. CUPULE smaller, ca. 10-12 mm long. CUPULE-APPENDAGES linear; ca. 4-6 mm long. NUTS with prominent wings along the angles.

3-3-5 F. TIENTAIENSIS

1B. CUPULE-PEDUNCLE stouter, more than 1 mm thick. CUPULE larger, ca. 12-30 mm long. NUTS without wings or at most with narrow wings along nut-angles.

2A. CUPULE-PEDUNCLE longer, ca. ((1))- (3)-4-6-(7) cm long. CUPULE larger, ca. 15-30 mm long. CUPULE-APPENDAGES linear; spreading to recurved; ca. ((4))- (8)-10-12-(15) mm long.

3-3-2 F. LONGIPETIOLATA

2B. CUPULE-PEDUNCLE shorter, ca. 1.5-1.8 cm long. CUPULE smaller, ca. 12-15 mm long. CUPULE-APPENDAGES subulate; sharply recurved; ca. 2.5 mm long.

3-3-4 F. BIJIENSIS

Fagus longipetiolata is the most common and first-published species among the four species of this section recognized in this monograph. Both F. bijiensis and F. tientaiensis are based on single trees. All of the three less common species are distributed well within

the range of F. longipetiolata. [The latter is the most widespread beech in China.] Roughly speaking, species of this section are readily distinguishable from those of the section *Lucida* by the lower surface of their leaves, which are glaucous and usually provided with short hairs, and their generally longer cupule-peduncles. Under a 30x magnification, the crowded rounded white dots are clearly visible. The reflection of the incident radiation from the surface relief of these species causes the visible glaucosity. [The surface detail of the taxa of the subgenus *Engleriana* is different under 30x magnification, though glaucosity also characterizes this entity.] As to the short hairs, they are clearly of a distinct category from the long hairs, which are present in very young leaves of all beeches and persistent to various degrees on mature leaves of some taxa. The generally longer cupule-peduncle is clearly a derived state within the subgenus. Its presence here should be regarded as representing the parallel development of this feature in the subgenus *Fagus*, compared with the subgenus *Engleriana*.

If the other three species were not present, the circumscription of the then monotypic section *Longipetiolata* would be far more clear and sharp, with regard to other sections. This section is obviously very far from the section *Grandifolia*, judging from almost all of the taxonomically important features at the sectional level. However, the short hairs on the lower surface of leaves of some plants of the section *Grandifolia* cannot be distinguished from the short hairs of this section. As to the relative distance to the remaining two sections, this section is obviously closer to the section *Lucida*, in both leaf and cupule features.

3-3-2 FAGUS LONGIPETIOLATA SEEMEN

Fagus longipetiolata Seemen, (1897 Aug), Bot. Jahrb. 23, Beibl. (57):

56. [SYNTYPES: A. Henry 5334, E!, G(2)!, GH!, K (Color photo)!, US-801056 !; A. Henry 5334-A, A(2)!, E!, G!, GH!, K (Color photo)!, US-598673 !, US-801057 !)]

Fagus sylvatica L. var. longipes Oliver, (1890), in Hooker, J.D., Ic.

Pl. 20: sub pl. 1936. [SYNTYPES: A. Henry 5334; A. HENRY 7444, K (Color photo)!, GH!, US-802090 !]

Fagus sinensis Oliver, (1890), in Hooker, J.D., Ic. Pl. 20: sub pl. 1936, in tabula tantum.

Fagus clavata Y.T. Chang, (1966 Apr), Acta Phytotax. Sin. 11: 119-120, Pl.18. [HOLOTYPE: Z.S. Chang & Y.T. Chang 4870; PE, n.v.]

HIGH-BRANCHING TREES, to 30 m tall, 1 m DBH. BARK smooth and whitish/silvery, lenticels inconspicuous. CURRENT-YEAR SHOOTS stout, generally more than 1 mm thick; brownish to purplish; glabrous. BUDS sessile; ovoid to cylindric; with a blunt apex; sometimes the upper margin of the upper bud-scales hairy; 4-6 x 2-4 mm at the end of the growing season. LEAVES (narrowly ovate) to ovate/trullate to oblong to ((elliptic)); 8-12-(15) cm long; thick-chartaceous. APEX acuminate to (acute). BASE broadly cuneate to narrowly cuneate to concave. UPPER SURFACE dark green. LOWER SURFACE glaucous; often covered with short, white hairs to various degrees. SECONDARIES 12-15-(18); generally

terminating a tooth-tip, but an abruptly upward branch also present. Primary/secondary POCKET-DOMATIA present. MARGIN (slightly crenate) to slightly denticulate to slightly serrate. PETIOLE generally 1/6-1/8 as long as the leaf-blade.

Flowers per MALE INFLORESCENCE ca. 15-31. Hairs on the upper part of the PERIANTH-TUBE normally eglandular; whitish/yellowish. FRUIT MATURING in late July to early August. CUPULE-PEDUNCLE thick, generally thicker than 1 mm; ((1))-(3)-4-6-(7) cm long; generally glabrous. CUPULE-VALVES oblong; with the tip generally rounded; thick; ca. 15-30 mm long. CUPULE-APPENDAGES hairy; linear; ((4))-(8)-10-12-(15) mm long; when shorter mostly spreading, when longer recurved, sometimes recurving back again to a sigmoid shape. NUTS generally with discernible wings along the angles, rarely without, or rarely with conspicuous wings; generally level with the cupule-valves. CHINA.

LECTOTYPIFICATION:

LECTOTYPE: A. Henry 5334, CHINA, Hubei-Badong; K! (in color-photo form, the specimen housed in K not seen)

ISO-LECTOTYPES: E!, G(2)!, GH!, US-801056 !

Since the collection A. Henry 5334 is among the syntypes of each of the three earliest names of this species, it is here designated as the lectotype of F. longipetiolata.

The specific epithet refers to the generally longer petiole of this species, compared with all other beech species known to the author. This still holds true.

ILLUSTRATIONS:

Oliver (1890: pl. 1936); Hu & Chun (1927: pl. 17); Chang (1966: pl.18); Anonymous (1972: Fig. 816); Anonymous (1980: Fig. 183); etc.

DISTRIBUTION AND ECOLOGY:

Fagus longipetiolata is the most widespread beech species in China [see the distribution maps in Tsien et al. (1975: 11; prepared by Y.-T. Chang) and Chang (1981: 49)]. Its range approximately represents the entire range of beeches in China. A notable exception is in the most southeastern corner of the latter - Taiwan, where F. hayatae subsp. hayatae is the only beech. Fagus longipetiolata grows within an altitudinal range from 500 m to ca. 2,000 m. Because of its broad geographical range and its low altitudinal limit, F. longipetiolata is the most familiar beech to Chinese. The Chinese name of beeches, Shuei-Ching-Gang, is supposed to have been based on this species. In this sense, it could be called "the common Chinese beech".

All Chinese beeches are mountain-inhabitants. Although F. longipetiolata can grow up to ca. 2,000 m alt., its populations are centered within a range of ca. 700-1,500 m alt. Around its lower limit, this species has individuals scattered in forests chiefly composed of evergreen trees of Fagaceae, Lauraceae, Theaceae, Ericaceae, Symplocaceae, Aquifoliaceae, etc. Most of these families have their cold-tolerant (evergreen) members growing up to ca. 1,800 m alt., where F. longipetiolata is rare but F. engleriana becomes common. What I wish to emphasize here is: in China, F. longipetiolata is a prominent deciduous hardwood tree which can do well in a subtropical climatic

regime. In this regard, it is similar to many deciduous members of Hamamelidaceae, notably Liquidambar formosana. At some localities of a higher elevation, ca. 700-1,200 m, and well within the northern subtropical (or upper oromeridional) bioclimatic subzone, F. longipetiolata is a codominant species. Above this subzone, that is, in the "Mixed Mesophytic Forest" vegetation zone, it is common everywhere but nowhere abundant. And it is within this zone that it occurs with F. brevipetiolata, or F. lucida, or F. hayatae subsp. pashanica. However, I am not aware of any localities where this species grows with F. engleriana. When these two species are sympatric, they are separated by a belt of other trees. When any other beech species is present in this belt, which is not uncommon, some level of competition between congeneric species can explain this belt-like altitudinal distribution of three congeneric species. When no other beech species is present in between, this altitudinal discontinuity denotes a discontinuity in ecological amplitude between these two species. Thus, the optimal adaptational range of F. longipetiolata is largely, if not entirely, within the northern Subtropical bioclimatic subzone, similar to the situation of F. japonica.

TAXONOMIC REMARKS:

The first name referring to the plants of this species is Oliver's F. sylvatica var. longipes, published in 1890. However, he also used another name, F. sinensis, for the line-drawing of this new plant. Later authors working on the Chinese beeches handled this nomenclatural issue differently. Seemen published another name, F.

longipetiolata, in 1897, without listing any synonym; but one of Seemen's two syntypes (A. Henry 5334) had been cited by Oliver as one of his two syntypes. Franchet took Oliver's varietal name and listed Oliver's specific name as the only synonym, in 1899 (July). Skan followed Franchet, and added Seemen's specific name as the second synonym, in 1899 (Dec). Seemen & Diels took Oliver's specific name F. sinensis, and listed two synonyms: F. sylvatica var. longipes and F. longipetiolata. With reference to the basic concept of the type method and priority, it would be natural that a later worker can take F. sylvatica var. longipes if the varietal status is considered proper for this plant, or take F. sinensis if he regards this plant as a distinct species. Unfortunately, the last and most influential Euramerican authors working on the Chinese Fagaceae, Rehder & Wilson, took F. longipetiolata in 1916. To follow the most common current usage and to avoid unnecessary nomenclatural change, I use the name F. longipetiolata for this species.

With about 80 fruiting collections available for observation, I can detect three major groups: northern, southern, and eastern ones. The type collection is from the northern group and well represents this group in its critical taxonomic features. The populations of this group are centered in W Hubei, W Hunan, and Sichuan. It is characterized by mostly oblong leaf-shape, more prominently serrate margin with concave sinuses, lower leaf-surface generally with abundant short eglangular hairs and some yellowish glandular hairs, larger cupules, and generally unwinged or only weakly winged nuts. The southern group is distributed in Gueizhou, E Yunnan, N Vietnam, N Guangxi, and N Guangdong, and is

recognizable by the mostly trullate and more slender leaf-shape, lower leaf-surface with fewer short eglandular hairs and abundant yellowish/reddish glandular hairs, larger cupules, and generally winged nuts. The eastern group is geographically more well defined and more isolated. It occupies the eastern range of the species, that is, S Anhwei, Zhejiang, E Jiangxi, and W Fujien; and has mostly ovate leaf-shape, more denticulate margin with often convex sinuses, lower leaf-surface with abundant short eglandular hairs and some yellowish/reddish glandular hairs, smaller cupules, and generally unwinged or only weakly winged nuts. The geographical boundary between the northern and the southern groups is vague. This is not surprising at all because there is no clear topographical barrier in that general region.

The overall condition of the differentiation of these three groups is roughly comparable with that of the three American beeches. However, the infraspecific taxonomic decision for the latter is easier to make, due to the difference in cupule-appendages between the northern Gray Beech and the southern White Beech, the geographical disjunction between the latter and the Mexican Beech, and the ecological differences among the three. Nevertheless, if desired, at least the eastern group of F. longipetiolata could be segregated as a distinct subspecies, chiefly based on the distinct appearance of its leaves and its more sharply defined range. No name is currently proposed for the eastern group.

Chang (1966: 119) published a forma of F. longipetiolata: forma yunnanica, and indicated that it is distinct in its "shorter peduncle, 1.5-2.5 cm long, ascending; ovato-lanceolate leaves". All of the six

collections cited by him are from the southern range of my southern group. Though I have had no chance to examine the type collection, specimens of two paratypes are at my disposal. They can be lumped into the pile of the specimens of my southern group, even without the reference of their geographical origin. The only peculiar trait shown by them is indeed the extraordinarily short cupule-peduncle. The only other two collections from N Vietnam (unseen by Chang) resemble the previous two in almost every detail. As a preliminary conclusion, it is very likely that there indeed exists an entity in the most southwestern range of F. longipetiolata, which is distinctive at least in its very short cupule-peduncle.

Chang (1966: 119-120, pl. 18) proposed a new species F. clavata, indicating that it has affinities to F. longipetiolata and F. brevipetiolata but differs from them in its "stouter and shorter peduncle, 1-1.5 cm long, dilated from the base to the top". Only two collections were cited in his work, including the type. Both are from a limestone mount, Longtoudashan, in Guizhou. Although the type collection of this species is not now available to me, the description and the line-drawing of the type are very helpful. The characteristics of this species, as shown by the type collection, are not significantly different from those of Chang's forma yunnanica, except the following three respects. First, the cupule-peduncle (of the former) is shorter. Second, the leaf-shape is ovate to ovate/lanceolate. Third, the sinuses of the leaf-margin are slightly convex. Uniformly short cupule-peduncles to the extent as shown by these two groups are not present elsewhere within the range of F. longipetiolata, to my knowledge. The

last two traits make it better to include F. clavata within the southern, rather than the northern group of F. longipetiolata. This treatment is also more in accord with its geographical location: the northern portion of the range of the southern group.

Chang & Huang (1988: 114) listed Chang's forma yunnanica as a synonym of F. longipetiolata, and reduced F. clavata to a forma of F. longipetiolata. They recognized no infraspecific taxa within F. longipetiolata except the forma clavata. They regarded almost all variations observed on the plants from the limestone mountains in Gueizhou, Guangxi, and Yunnan, which have resulted in the publication of all of the names botanically associated with F. longipetiolata, as simply representing variations at the ecotypic level. Leaving the taxonomic treatment aside, I do not agree with their perception on these variants. It is clear that population research should be done before a satisfactory infraspecific treatment of F. longipetiolata can be presented. Discussions on the infrasectional evolution is available in 3-3-5.

3-3-3 FAGUS BREVIPETIOLATA HU

Fagus brevipetiolata Hu, (1951 Mar), Acta Phytotax. Sin. 1: 103-104.

[HOLOTYPE: K.M. Feng 13815, PE, n.v.; ISOTYPE: A!]

DECIDUOUS TREES. CURRENT-YEAR SHOOTS slender, ca. 1 mm thick; light-colored, yellowish/brownish. BUDS slender-fusiform; with an acute

apex; ca. 6-10 x 1-2 mm at the end of the growing season. LEAVES narrowly ovate-lanceolate; 10-12-(15) cm long; thin-chartaceous. APEX acuminate-caudate. BASE rounded to broadly cuneate. UPPER SURFACE dark green. LOWER SURFACE glaucous; with short unicellular hairs, without glandular hairs. SECONDARIES (10)-12-15-(18); generally ending at the tip of a tooth, but with an abruptly upcurved branch just short of the margin. Primary/secondary POCKET-DOMATIA present. MARGIN slightly serrate to slightly denticulate. SINUSES slightly convex to slightly concave. PETIOLE ca. 1/10-1/12 as long as the leaf-blade.

REPRODUCTIVE FEATURES unknown. CHINA.

HOLOTYPE:

K.M. Feng 13815, CHINA, Yunnan-Malipuo; PE, n.v.; ISOTYPE: A!

The specific epithet refers to the very short petiole of this species, relative to the length of the leaf-blade. The ratio of petiole to leaf-blade of this species is the smallest among all beech taxa, together with F. grandifolia.

ILLUSTRATIONS:

None.

DISTRIBUTION AND ECOLOGY:

Hu described this species on the basis of a single collection from Yunnan. Chang (1966: 120) cited four more collections from Sichuan, Hunan, Gueizhou, and Yunnan, respectively. Among these five, two are available to me, including the type; the second one, Y. Tsiang

5457, was cited as Y. Tsiang 2457 by Chang. Based on these two specimens and the two published descriptions, I identified several more specimens as this species. They are from Guangdong (one specimen) and the eastern portion of Dabashan Range (W Hubei and NE Sichuan; see 2-5-1). Both Henry and Wilson had collected extensively in the eastern portion (W Hubei) of the latter region. Wilson's numbers AA-493, AA-700-A, and AA-700-B are mixed collections of F. longipetiolata and F. brevipetiolata. They are all from Badong of Hubei. A mixed stand composed of F. brevipetiolata, F. hayatae subsp. pashanica, F. engleriana, and other evergreen trees in the western portion (NE Sichuan) of the latter region was observed by my colleague GE Ji-Wen, and the populations of beech species were sampled, by Ge, at my request. The populations of F. brevipetiolata seem to be centered in the western portion of the range of F. longipetiolata. Its altitudinal range is also well within that of F. longipetiolata, according the very limited information in this respect (1,450 m, NE Sichuan; 1,250 m, Sichuan/Hubei; 1,000-1,800 m, W Hubei; 400-550 m, C Gueizhou; 1,500-1,700 m, SE Yunnan).

TAXONOMIC REMARKS:

Although the vegetative features as observed on specimens can sharply separate the specimens here identified as F. brevipetiolata into their own pile, there are two extremely troublesome matters with the taxonomy of this species. First, I have seen no specimens whose vegetative features are definitely of F. brevipetiolata-type with a physically attached cupule/nut complex. Second, at least three of the

eight collections were made from sprouts or small trees, according to the field-notes.

It may be proper to copy the pertinent fieldnotes of the available collections of this species as follows:

J.W. Ge, Nanjiang-2-2, Sichuan-Nanjiang, 1988-10-27; "1,450 m, 3 m tall, collected from sprouts, fruits not seen." (NY)

J.W. Ge, Nanjiang-2-3, Sichuan-Nanjiang, 1988-10-27; "1,450 m, 2.5 m tall, collected from sprouts, fruits not seen." (from the same population as the above collection; NY)

Y. Tsiang 5457, Gueizhou-Gueiding, 1930-6-30; "400-550 m, in dense shade, a small tree, 2 m tall, sterile." (NY)

J.L. Gressitt 2467, Hubei-Lichuan, 1948-7-29; "Shueishanba, hill, ridge, 1,250 m, a tree, 16 m x 30 cm, trunk smooth." (sterile; A)

K.M. Feng 13815, Yunnan-Malipuo, 1947-12-13; "1,500-1,700 m, in mixed forests, a tree, 40 ft tall, common." (with cupules and nuts collected from the ground, contained in a parcel; Isotype, A)

W.Y. Chun 5962, Guangdong-Mahang, 1927-12-27; "in open side of the road, on knoll, a tree, 18 m, bark gray, smooth, fruit separate." (with a single empty cupule fixed on the sheet; A)

Collector and locality unknown, a sterile branchlet, in K; photo taken by R.C. Ching, in NY.

C. Schneider (1916-9-18), a sterile branchlet, collected in the Arnold Arboretum, from an individual with the accession number Wilson 7000. (US-1523753)

The cupules and nuts of the type collection look similar to the ordinary ones of F. longipetiolata, though the former are a bit abraded. If the type locality is considered, then they are probably more similar to those of the southern group of F. longipetiolata, at least in their shorter cupule-peduncle (1.5-3 cm long). The single empty cupule of the Guangdong collection is indeed peculiar in its short appendages (ca. 3-4 mm), but it otherwise resembles cupules of F. longipetiolata. If the cupules associated with these two collections indeed belonged to the individuals collected as specimens, then the taxonomic status of these plants can be considered in a different way.

The vegetative characteristics of F. brevipetiolata, as observable on the specimens, are so distinct that the sterile specimens of this species can be readily sorted out from the pile of sterile specimens of all beech species. In a genus-scale comparison, the taxonomic distribution of the diagnostics of the leaves of F. brevipetiolata reveals some interesting facts. First, the often lanceolate leaves with a long-acuminate apex and a rounded base are only seen in many Mexican beeches elsewhere within the genus. Second, the very short (relative to the leaf-blade) petiole is also a characteristic of F. grandifolia. Third, the eglandular short hairs on the lower leaf-surface are again found in many American beeches. Fourth, the glaucous lower leaf-surface is an autapomorphy of the section Longipetiolata. The glaucosity of the leaves of the subgenus Engleriana is regarded as a convergence (see 3-2).

The characteristics of the current-year shoots are somewhat variable, and therefore perhaps not very reliable as taxonomic markers

for F. brevipetiolata. The situation of buds is similar, because the buds of F. longipetiolata-type are found in a few specimens of F. brevipetiolata. It is arguable that sun-buds are certainly more slender and fusiform compared with the generally more ovoid and shorter floral buds (and shade-buds to a lesser extent) (see e.g., Roloff, 1986: 10; among others), and that the shape and size of buds are not always suitable for taxonomic use due to their high variability. My argument in this respect is as follows. First, the general shape of buds is constant in nearly all of the major beech species, based on my observations on the specimens under study, although their size may be associated with the size of the enclosed leaves to some extent. Second, the differences between sun-buds and floral buds are not significant enough to restrict the utilization of the bud features in taxonomy of Fagus. Probably all beeches mast every three to five years. Even during the mast year not all shoots are floriferous. Third, the gross shape and size of the leaves of F. longipetiolata are not significantly different from those of, for example, F. japonica, in the eyes of a layman, but I have never seen a fusiform bud with an acute apex on a specimen of the former nor seen an ovoid bud with a blunt apex on a specimen of the latter. Fourth, similar comparisons could be made between F. longipetiolata and species of other sections within the same subgenus. Fifth, the shape and size of the buds of F. brevipetiolata are more similar to those of F. japonica (and F. engleriana) than to F. longipetiolata.

A few collections of F. brevipetiolata were made from sprouts or small trees (2-3 m), as mentioned above. The possible significance of

this point could be vitiated by the three collections made from large trees (12 m, 16 m, 18 m, respectively). Chang & Huang (1988: 114) regarded F. brevipetiolata as an ecotype of F. longipetiolata due to the dry habitat of the limestone mountains in Gueizhou, Guangxi, and Yunnan. The traits they referred to are the very short petiole of the "newly borne" (translation mine) leaves and the short peduncle. I am not quite clear about their "newly borne" leaves. The peduncle of that empty cupule from Guangdong is 4.5 cm long. The peduncles of the type collection are roughly as long as those of the entity named as forma yunnanica of F. longipetiolata. As a result, their idea can possibly explain the differentiation of the southern group of F. longipetiolata, but it is not applicable at all to the populations of F. brevipetiolata in W Hubei and NE Sichuan, including that in the classical locality of Metasequoia.

The "sterility" of all the specimens available for me could lead to a conjecture that F. brevipetiolata is a sterile hybrid. Since vegetative regeneration probably functions in all beech species, and sprout growth to 3 m high has been recorded for F. brevipetiolata, issues associated with reproduction and self-perpetuation could at least theoretically resolved. On the other hand, if that empty cupule, as mentioned previously, is indeed biologically affiliated with F. brevipetiolata, then its very short appendages are compatible with those typical for F. grandifolia. Taking the similarities in leaves between these two species into consideration, I would like to advance the speculation that these two species are genetically connected. If this is true, then the branching point of the section Grandifolia would be

closer to the section Longipetiolata than to other sections, within the subgenus *Fagus*.

It is not profitable to proceed with these speculations. In this respect, perhaps fossils could offer more information.

3-3-4 FAGUS BIJIENSIS C.F. WEI & Y.T. CHANG

Fagus bijiensis C.F. Wei & Y.T. Chang, (1966 Apr), Acta Phytotax. Sin.

11: 121, pl. 19. [HOLOTYPE: P.H. Yu 766, PE, n.v.; ISOTYPE: IBSC-343516 !]

DECIDUOUS TREE. CURRENT-YEAR SHOOTS stout, thicker than 1 mm; generally dark-colored and purplish/brownish. BUDS ovoid; with a blunt apex; ca. 4-8 x 2-4 mm in September. LEAVES generally ovate; thick-chartaceous. APEX acute. BASE cuneate. UPPER SURFACE dark green. LOWER SURFACE light green to slightly glaucous; with both short eglandular hairs and glandular hairs. SECONDARIES 10-12; each terminating in a tooth-tip. Primary/secondary POCKET-DOMATIA present. MARGIN simply serrate or compoundly serrate with only one inter-secondary tooth. PETIOLE long, ca. 1/6-1/8 as long as the leaf-blade.

CUPULE-PEDUNCLE stout, more than 1 mm in diam.; ca. 15-18 mm long. CUPULE-VALVES ca. 12-15 mm long. CUPULE-APPENDAGES subulate; ca. 2 mm long; recurved. NUTS wingless; roughly level with the cupule-valves. CHINA.

Based on one isotype and the original description.

HOLOTYPE:

P.H. Yu 766, CHINA, Gueizhou-Bijie; PE, n.v.; ISOTYPE: IBSC-343516 !

In Chinese (Mandarin), most words end in a vowel. The last vowel of any word is as important as any other sound of that word in distinguishing that word from other words. When transliterated into any other language for the sake of communication, the last vowel of a word should be kept unchanged. Following this principle, this specific epithet should be spelled as "bijieensis".

ILLUSTRATIONS:

Chang (1966: pl. 19).

DISTRIBUTION AND ECOLOGY:

Wei & Chang published this species on the basis of a single collection from Gueizhou. The type tree grows "in a thicket on the crest of a ridge, at 1,450 m alt." The locality is within the range of the southern group of F. longipetiolata. Chang & Huang (1988: 114) mentioned this locality as a limestone mountain, and included this individual in a comprehensive F. longipetiolata, with only one recognized infraspecific taxon, forma clavata, based on F. clavata (see 3-3-2 and 3-3-3). Naturally, they did not assign additional collections to the name F. bijiensis.

TAXONOMIC REMARKS:

There is only one specimen (isotype) at my disposal. At first

glance, it is similar to both F. lucida and F. longipetiolata. Its yellowish shoots are closer to those of F. lucida. (Two of the three current-year shoots of this specimen are purplish/brownish - the ultimate color of any light-colored shoots of any beech.) Its leaf-margin is closer to that of F. longipetiolata, but the occasional subsidiary teeth are not observed in F. longipetiolata. Its short eglandular hairs are characteristic of the section Longipetiolata. Its stout and short cupule-peduncle is comparable with those of the infraspecific entity of F. longipetiolata confined to the most southwestern corner of its range (see 3-3-2). However, it is also similar to those of some "abnormal" specimens of F. lucida. The size of its cupules is "normal" for F. lucida, but "abnormally" small for F. longipetiolata. Its thin and very short cupule-appendages are not seen on any Asian cupules of that size, but remind me of F. grandifolia subsp. caroliniana. The cupule-appendages of another species of the section Lucida, F. chienii, are obviously stouter, and should have derived from woody, thick and scale-like appendages such as those typical for F. lucida. Its wingless nuts are typical for F. lucida, and present in some specimens of F. longipetiolata.

If this individual is to be lumped with other individuals at the specific level, F. longipetiolata is clearly the name of that comprehensive species. Chang & Huang (1988: 114) ascribed the shorter peduncle, smaller cupule, and shorter appendages of this individual to the dry habitat of the limestone mountain. Their argument is not convincing to me. The size of the cupules is generally useful at the specific level, when it is applied with a sometimes considerable range

of variation. This is just the case of F. longipetiolata. I shall mention one fact in this connection: the entity named as forma yunnanica of F. longipetiolata has cupules among the largest ones of the species; this entity has short cupule-peduncles (1.5-2.5 cm, according to the original description; see Chang, 1966: 119), and grows on limestone mountains. The length of the peduncle varies with the size of its cupule and its position on a shoot, within an individual; and varies at various infrageneric levels. Nevertheless, it bears heavier taxonomic significance than the size of the cupule, because it tends to covary with some other taxonomic features sometimes even down to the subspecific level, such as in F. lucida and F. hayatae, and possibly also in F. sylvatica and F. grandifolia. As to the shorter cupule-appendages of F. bijiensis, it should be considered as of primary importance in its taxonomy. For any beech tree, given a cupule-valve and a typical leaf, I can identify this tree to species, with some difficulty only between some F. sylvatica and F. crenata. The extremely short cupule-appendages of F. bijiensis are not seen elsewhere within the section Longipetiolata. As has been addressed previously (see 3-2), the scale-like appendages are regarded as a plesiomorphy for the entire genus. I here consider the appendages of F. bijiensis to represent an intermediate step from scale-like appendages to the long linear ones typical for F. longipetiolata.

The occasional subsidiary teeth on the leaves of F. bijiensis are also not observed elsewhere within the section. They are otherwise present in F. lucida and F. hayatae (both of the section Lucida), within the genus. The development of this seemingly trivial trait needs a

prerequisite: the often convex sinuses, based on my observation. The highly convex sinuses, as usually seen in F. lucida, naturally prevent this development. On the leaves of F. hayatae, the sinuses normally vary from slightly convex to sinuous; it is in this species that the case of compound serration "normally" occurs, though not very often. A further interesting observation with the leaves of F. bijiensis is: if the whole leaf (including petiole) were reduced to the normal size of F. hayatae, I would be unable to tell it apart from the leaves of the latter without the reference of the hairs on the lower surface. Most probably only single leaves of the examined specimens of F. longipetiolata would pass this test.

Finally, I have no intention to suggest a hybrid status for F. bijiensis. A single specimen restricts any further speculation.

3-3-5 FAGUS TIENTAIENSIS T.N. LIOU

Fagus tientaiensis T.N. Liou, (1935 Dec), Contr. Inst. Bot., Nat. Acad.

Peiping 3: 451, pl. 43. [HOLOTYPE: S. Chen 3718, PE, n.v.; ISOTYPE: A!]

DECIDUOUS TREES. CURRENT-YEAR SHOOTS ca. 1 mm in diam.; light-colored, yellowish/brownish. BUDS slender-fusiform and with an acute apex, or narrowly ovoid and with a blunt apex. LEAVES ovate to elliptic; 6-8 cm long; thin-chartaceous. APEX acuminate. BASE rounded to cuneate. UPPER SURFACE dark green. LOWER SURFACE light green to

slightly glaucous; with both glandular hairs and short eglandular hairs. SECONDARIES 10-12; each terminating in a tooth-tip. Primary/secondary POCKET-DOMATIA present. MARGIN denticulate. SINUSES slightly convex. PETIOLE ca. 1/8-1/9 as long as the leaf-blade.

FRUIT MATURING no later than late July. CUPULE-PEDUNCLE slender, generally somewhat less than 1 mm in diam.; ca. 2-3 cm long. CUPULE small, ca. 10-12 mm long. CUPULE-APPENDAGES linear; ca. 4-6 mm long; recurved. NUTS level with the cupule-valves; with prominent wings along the angles. CHINA.

Based on two collections made from the type tree in different years (1934 and 1988) and the original description.

HOLOTYPE:

S. Chen 3718, CHINA, Zhejiang-Tientai; PE, n.v.; ISOTYPE: A!

ILLUSTRATIONS:

Liou (1935: pl. 43).

DISTRIBUTION AND ECOLOGY:

Camp annotated a few specimens of F. longipetiolata as this species, and discussed his identification in his manuscript. Those specimens fit well within the concept of the forma yunnanica of F. longipetiolata (see 3-3-2 and 3-3-4). Chang & Huang (1988: 115) said that "There are only two collections of this species since 1935 till now; both are said to be from the same type tree". In his revision of the Chinese beeches, Chang (1966: 121) cited two collections for F.

tientaiensis. That one other than the type collection is available to me (R.C. Ching 1451). It is unlikely to be from the type tree after a detailed comparison. On the other hand, it fits well within my concept of the eastern group of F. longipetiolata. A local taxonomist, LOU Lu-Huan, reported that he made the second collection from the type tree in late 1988. Lou's collection, at first glance, looks like specimens of my eastern group of F. longipetiolata to some extent, not surprisingly. A careful comparison reveals that this collection is very similar to the type collection. The only appreciable difference is found in the buds: those of the type collection are shorter and more ovoid, while those of the new collection are longer and more fusiform. The difference in collecting date could probably account for this (Aug. 8, vs. Sept. 28). Therefore, I accept this new collection as being from the type tree.

Here I copy the pertinent portion of the only available field-notes about this species (L.H. Lou 6064): "in forest by a gully; 500 m alt.; a tree, 15 m x 50 cm; bark slightly brownish, smooth; fruits are already fallen, those picked up from the ground are abraded and turned grayish brown." (translation mine). In the same mountain region (Tientaishan Mt.), F. longipetiolata is "fairly common" at ca. 600-700 m alt. (R.C. Ching 1451; 1476; Y. L. Keng 1081). It is notable that three of the six associated trees are evergreen, and a common bamboo is growing there; but no individuals of F. longipetiolata were observed.

TAXONOMIC REMARKS:

This species can be characterized by its elliptic and thin-chartaceous leaves with denticulate margin and slightly convex sinuses,

presence of both glandular hairs and short eglandular hairs on the lower leaf-surface, long petiole, short peduncle, small cupules, linear appendages, and the prominently winged nuts. This diagnosis seems to be a combination of the characteristics of F. longipetiolata, and F. hayatae, in addition to those unique to this species. The elliptic and thin-chartaceous. leaves are not found elsewhere within this section or the section Lucida. Its margin and sinuses could be seen in the eastern group of F. longipetiolata, and are rather common in F. hayatae. The long petiole is a characteristic of both of these two sections. The overall appearance of its cupule (including peduncle) is intermediate between F. longipetiolata and F. hayatae. In other words, if all of the details of the cupule of F. longipetiolata are reduced by a certain fixed proportion, one will have a cupule probably not distinguishable from that of F. tientaiensis, just as when those of a cupule of F. hayatae are enlarged in the same manner. Such a cupule is, however, only found in F. tientaiensis. Finally, the prominently winged nuts of F. tientaiensis are very rarely seen in F. longipetiolata but is typical for F. hayatae.

If such a single-tree species is not accepted, then of course the name F. longipetiolata would be proper for this tree, if the short eglandular hairs on the lower surface of the leaves of this tree and the comprehensiveness of F. longipetiolata are considered. Chang & Huang (1988: 115) suspected the type tree to be simply an ecotype of F. longipetiolata due to its sole presence. This idea is unacceptable to me. A vertical distance of one hundred meters is negligible for a species with a broad ecological amplitude except on the margin of its

adaptation. Fagus longipetiolata occurs at 400 m alt. even in its southern range. The two collections from the type tree show the same peculiar traits whose adaptational significance does not come to my mind at all. The type tree is situated in a general region where hybridization between F. hayatae and F. longipetiolata could be reasonably supposed to have occurred in the past. However, the elliptic and thin-chartaceous leaves of F. tientaiensis do not allow me to think further about this possibility, because they are not present elsewhere within the two sections embracing the two supposed parental species. I would rather retain the specific status for this single tree at this time for both theoretical and practical purposes.

Before closing the section Longipetiolata, it will be interesting to discuss the speciation and subspeciation of the taxa involved here. All of the three small species, or satellite species, occur within the range of F. longipetiolata. More precisely speaking, each of them is sympatric with F. longipetiolata, and the altitudinal differences between each of them and the major species, if present, are nearly negligible. For these wind-pollinated and self-sterile trees, if the genetic distinctiveness of such small species is to be maintained, a reasonably sharp isolation in anthesis from the sympatric major species is necessary. Unfortunately, no information about the flowering period of the three satellite species is so far available. With regard to the major species itself, the few flowering specimens are not enough to establish the antheses of the major infraspecific entities. Nevertheless, the geographically more isolated eastern group had developed its autapomorphies and/or maintain some symplesiomorphies of

the species, under a more favorable condition.

In discussing the evolution of the critical features within such a closely knit group, it is useful to consider the (at least) three infraspecific entities of F. longipetiolata discussed above and the three satellite species as individually equivalent. Following this approach, I would like to propose a set of traits for a hypothetical ancestor of the section as follows: ovoid buds; medium-sized, ovate and thick-chartaceous leaves with slightly serrate margin, slightly concave sinuses and both glandular and short eglandular hairs on the glaucous lower surface; short cupule-peduncle; small cupule; subulate (or at most short linear) cupule-appendages; and wingless nuts.

F. brevipetiolata may be immediately removed from the coming evaluation, although I consider it to be a member of the section under enquiry. If it is of hybrid origin between some members of the section Longipetiolata and the section Grandifolia, it should be more similar to the northern members of the section Grandifolia. This is not the case. If it represents the "relic" element from the common ancestry of these two sections, solid fossil evidence is necessary. This cannot be proved at this moment. In considering the remaining "entities", long petiole is to be added to the list of the symplesiomorphies of the group.

The contest is finished immediately. Fagus bijiensis is undisputably closest to the supposed ancestor. It deviates only in its gross leaf appearance. This deviation is not pertinent to the circumscription of the section Longipetiolata, while it most probably represents a parallel development to the section Lucida. If the habitat of the type tree of F. bijiensis is not very different from the norm, at

least the drier and more exposed limestone site should be allright for the ancestral members of the section, given enough atmosphere humidity. [Gueizhou Province is famous or notorious in its very high relative humidity, as strongly expressed in a proverb: "You cannot have three consecutive sunny days in Gueizhou.".] Within F. longipetiolata, the southern group is perhaps closer to the ancestor of the species than both the northern and the eastern groups. However, F. tientaiensis is very hard to explain even within this theoretical frame. If it did not have eglandular short hairs on the glaucous lower surface of its leaves, it would be best kept in the more loosely defined section Lucida. Returning to F. brevipetiolata, if it did not have glaucous lower leaf-surface, its vegetative traits at the branchlet level would send it into the section Grandifolia. These two issues are left unresolved.

3-4 SECTIONS OF THE SUBGENUS FAGUS: SECTION LUCIDA SHEN, SECT. NOV.

3-4-1 KEY AND DISCUSSION OF THE SECTION

A diagnosis of this section within the subgenus has been offered in the synoptical key to subgenera and sections (see 2-3). A synoptical key to the series of this section is given as follows.

1A. CUPULE-APPENDAGES linear, the basal ones often spatulate-foliaceous.

CUPULES 1.5-2.5 cm long. CUPULE-PEDUNCLE (1.5)-2-3-(4) cm long. NUTS generally somewhat winged, and generally level with the cupule-

valves. LEAVES generally broadly ovate-elliptic; (6)-8-10-(12) cm long. LOWER SURFACE often with long, silky hairs on the major veins. MARGIN crenate to sinuous to slightly serrate. SINUSES generally sinuous if present. JAPAN.

Series CRENATAE

1B.CUPULE-APPENDAGES either scale-like or subulate or linear. CUPULES ca. 1-1.5 cm long. CUPULE-PEDUNCLE (0.5)-0.8-1.2-(1.5) cm long. NUTS either wingless or prominently winged; slightly to well exerted from the cupule-valves. LEAVES generally narrowly ovate, sometimes ovate or oblong. LOWER SURFACE without long, silky hairs. MARGIN sharply denticulate. SINUSES prominently convex to slightly convex to (sinuous). CHINA.

2A.CUPULE-APPENDAGES scale-like or subulate, woody. NUTS normally wingless. LEAVES larger, (5)-7-10-(12) cm long. CUPULE-PEDUNCLE longer, ((0.5))-1-1.5-((1.8)) cm long. CUPULES larger, 1-1.5 cm long. NUTS generally at least somewhat exerted from the cupule-valves.

Series LUCIDAE

2B.CUPULE-APPENDAGES linear, recurved. NUTS always prominently winged. LEAVES smaller, (4)-5-8-(10) cm long. CUPULE-PEDUNCLE shorter, (0.5)-0.8-1.2-(1.5) cm long. CUPULES smaller, ca. 0.8-1.2 cm long. NUTS always well exerted from the cupule-valves.

Series HAYATAE

This section is more loosely organized than the other three

sections of the subgenus. Fagus lucida and F. hayatae are completely different in cupule-appendages, but very similar in leaves. The type collection of F. lucida is a mixture of sterile branchlets of these two species. Several earlier and sterile collections of F. hayatae from the general region of the type locality (W Hubei) were misidentified as F. lucida. However, within F. hayatae, the leaves of the subspecies hayatae are smaller than the other subspecies pashanica, which is the one having leaves sometimes hardly distinguishable from those of F. lucida. The overall situation is highly comparable with that of F. japonica and F. engleriana of the subgenus Engleriana, regardless of whether other features are taken into consideration or not.

If F. crenata were a small species or simply not existent at all, this section would be more elegantly defined and would be more evidently related to the section Longipetiolata (see 3-3-4 and 3-3-5). With regard to the often crenate or sinuous leaf-margin of F. crenata, at least two points could be presented to argue for the strong relationship between F. crenata and the previous two species. First, the pattern typical for the leaves of the previous two species is also found in occasional specimens of F. crenata, and intermediate patterns are commonly seen. Second, a complete transformation series of leaf-margin morphology, from slightly serrate to slightly crenate, is available within one beech species: F. sylvatica. Although this latter series does not show an intermediate stage which is typical for F. lucida and F. hayatae, it does demonstrate an evolution connecting serrate and crenate leaf-margin within the genus Fagus. The often spatulate-foliaceous basal cupule-appendages of F. crenata can only be interpreted

as derived, if the scale-like appendages of the trigonobalanoids are regarded as very close to the ancestral state of the whole family, and those of F. japonica and F. lucida are taken as ancestral to the whole genus. As a result, these three East Asian species should be considered as constituting a group within the subgenus *Fagus*.

As has been stated in the beginning of this discussion, this section is more loosely organized. This is chiefly attributable to the more diverse evolution of the cupule-appendages and the broader amplitude of the variation of the leaf-margin, compared with the other three sections. When this section is subdivided into three series, both the distribution range and the amplitude of internal variation of each of them will be smaller than any of the other three sections. If this section were maintained unsubdivided, its internal variation would be larger than that of the subgenus *Engleriana*. However, a subdivision is proposed here, chiefly because of the recognition of satellite species of at least F. lucida.

The keys to species and subspecies of each series are offered as follows.

KEY TO SPECIES OF THE SERIES LUCIDA:

1A. CUPULE-APPENDAGES subulate, recurved. **LEAVES** elliptic to narrowly ovate. **APEX** with a shorter, broader, and blunter tip.

3-4-3 F. CHIENII

1B. CUPULE-APPENDAGES scale-like, mostly appressed. **LEAVES** (oblong) to (elliptic) to trullate to ovate to (lanceolate). **APEX** with a longer, narrower, and sharper tip.

3-4-2 F. LUCIDA

KEY TO SPECIES OF THE SERIES HAYATAE (= KEY TO SUBSPECIES OF F.

HAYATAE):

1A. LEAVES ovate to (narrowly ovate); larger, (3)-5-8-(10) cm long.

CUPULE-PEDUNCLE longer, ca. 1-1.5 cm long. Mainland China.

3-4-4a F. HAYATAE subsp. PASHANICA

1B. LEAVES (ovate) to narrowly ovate to trullate; smaller, (2)-3-5-(6) cm long. CUPULE-PEDUNCLE shorter, ca. 0.6-1.2 cm long. Taiwan.

3-4-4b F. HAYATAE subsp. HAYATAE

KEY TO SPECIES OF THE SERIES CRENATAE (= KEY TO SUBSPECIES OF F.

CRENATA):

1A. STIPULES caducous. LEAVES larger, (5)-7-10-(12) cm long; broadly ovate to ovate to rhombic to broadly trullate. MARGIN seldom undulate. Hokkaido and Honshu (except the southeastern part).

3-4-5a F. CRENATA subsp. CRENATA

1B. STIPULES persistent. LEAVES generally smaller, (3)-4-6-(8) cm long, broad, ovate to rhombic to trullate (common); or narrowly elliptic to fusiform (rare). MARGIN sometimes undulate. Southeastern part of Honshu, Shikoku, and Kyushu.

3-4-5b F. CRENATA subsp. UNDULATA

3-4-2 FAGUS LUCIDA REHDER & WILSON

Fagus lucida Rehder & Wilson, (1916 Aug), in C.S. Sargent, Pl. Wils. 3:

191-192. [TYPE COLLECTION: E.H. Wilson AA-715, A(2)!, US-777132 !]

DECIDUOUS TREES; to 25 m tall, 1 m DBH. BARK whitish/silvery; smooth. CURRENT-YEAR SHOOTS light-colored, yellowish/brownish; sometimes hairy; thick. BUDS sessile; ovoid, with a blunt apex; ca. 4-6 mm long by the end of the growing season. LEAVES (oblong) to ovate to narrowly ovate to (lanceolate/trullate); (5)-6-8-(10) cm long; thick-chartaceous. APEX acuminate to (caudate). BASE broadly cuneate to narrowly cuneate to (concave). UPPER SURFACE dark green, lustrous. LOWER SURFACE light green, lustrous. SECONDARIES 10-12-(15); always terminating in a tooth-tip. Primary/secondary POCKET-DOMATIA always present. MARGIN always denticulate. SINUSES prominently to slightly (seldom) convex. PETIOLE ca (1/6)-1/8-(1/10) as long as the leaf-blade.

Flowers per MALE INFLORESCENCE 15-31. The hairs on the upper portion of the PERIANTH-TUBE eglandular; yellowish. FRUIT MATURING in late July to early August. CUPULE-PEDUNCLE generally short and stout; normally ca. (0.5)-0.8-1.2-(1.5) cm long and more than 1 mm thick, but rarely ca. (0.5)-1.5-2 cm long and less than 1 mm thick. CUPULE-APPENDAGES normally scale-like, large, thick, and appressed, but rarely very small, membranous, and erect. NUTS normally plump and wingless; slightly to prominently exserted from the cupule-valves. CHINA.

LECTOTYPE:

E.H. Wilson AA-715-A, CHINA, Hubei-Xingshan; A!; PARATYPES: E.H. Wilson AA-715-C & D, A!, E.H. Wilson AA-715-E, US-777132 !

Some of Wilson's collections on Chinese plants were taken from more than one individual, like those of Henry. For deciduous plants, collections combining flowering material and fruiting material of "the same" individual were normal in earlier times. When collecting is made in a remote and not readily accessible localities, this practice will produce many "population collections". When those localities are within a rich floristic region, this practice will easily result in collections composed of more than one species. If the collector maintains a "population concept", which is a very old tradition, several individuals belonging to more than one species could appear in a single collection. This is just the case of the type collection of F. lucida.

The type collection of the name F. lucida is sterile. Three sheets of the type collection are available to me. Two are from A and the third one is from US. Each of the two sheets from A has two branchlets (or an entire seedling). Unavoidably, I gave each of these branchlets a subnumber. The one I assign as 715-A is a sterile branchlet of F. lucida. Another sterile branchlet on the same sheet was assigned as 715-B; it is a F. hayatae subsp. pashanica. The collection 715-C is a seedling of F. lucida, which is about seven-years old. The collection 715-D is a sprout shoot of F. lucida, with many very large and very broad leaves supported by very short petiole. The single sterile branchlet on the US sheet (715-E) is a F. lucida, but this individual is most probably from a population different from that containing the 715-A individual. Wilson's Chinese collections generally have many duplicates housed in the Euramerican herbaria (but none in China). On duplicates from only A and US, at least three individuals of

F. lucida and one individual of F. hayatae subsp. pashanica are represented. I here designate 715-A (in A) as the lectotype of the name F. lucida. If this lectotype is lost, however, neither 715-C or 715-D or 715-E should be considered, because they are either a seedling or a sprout shoot or a branchlet only bearing very untypical leaves.

The specific epithet refers to the lustrous surfaces of the species.

ILLUSTRATIONS:

Hu & Chun (1933: pl. 130); Anonymous (1972: Fig. 817).

DISTRIBUTION AND ECOLOGY:

Since this species is the last Chinese beech species to be discussed here, and because it occurs almost throughout the whole geographic range of Chinese beeches, discussion of the overall distribution and the comparative ecology of Chinese beeches may begin here.

Distribution maps of F. lucida are available in Tsien et al. (1975: 11, prepared by Y.T. Chang) and Chang (1981: 49). Chang's 1981 map functions as a good starting point of my comparison. First, all these three major species show a latitudinally oriented ovate range, with the broader end on the west. The ranges overlap extensively, chiefly in SE Sichuan and W Hubei, so that the whole Chinese range of the genus is likewise ovate and latitudinally oriented. Second, F. engleriana forms the northern limit of the genus, and has the shortest N-S extent. Third, F. longipetiolata forms the southern limit of the

genus, and has the longest N-S extent. Fourth, F. lucida does not reach either limit, and has the medial N-S extent among the three. Fifth, the western limits of the three species are almost the same, and roughly parallel to the longitudinal line of 103 degrees E, in Sichuan. Sixth, in the northwestern range (including the northern limit) of the genus, chiefly in Sichuan, F. engleriana predominates over the other two. The Chinese specimens at my disposal offer quantitative support for this distribution pattern. Moreover, most of the populations of F. engleriana are centered in this region, based on my study. Seventh, in the southwestern range (including the southern limit) of the genus, chiefly in SE Yunnan, Gueizhou, SW Hunan, and N Guangxi, F. longipetiolata is more abundant than F. lucida, while F. engleriana is not present at all. Moreover, it is most probably in this region that F. longipetiolata is most heavily used as an important timber species, compared with other regions within its range, due to its abundance. Eighth, in the eastern range of the genus, in Zhejiang, NE Jiangxi, and S Anhui, F. engleriana shows a disjunct distribution (from its western range, see 3-1-2), while the continuously distributed F. lucida stops outside this region.

The discussions on the distribution presented immediately above have a direct implication on the comparative ecology of the Chinese beeches. Tsien et al. (1975) published a marvelous integrated study on the ecology and the phytochorological (= phytogeographical) significance of the beech forest in Fanjingshan Mt. (ca. 28 degrees N and 108.5 degrees E), in NE Gueizhou. This montane block is situated a bit north of the southern margin of the overlapping area of the three beeches, but

the several major peaks are fairly high (2,300-2,600 m), hence the three beeches are all represented there. They discussed the phytosociological differentiation in four zones, based on the differences in slope-facing and relative east-west location. It would be convenient to mention first that the beech forests are almost the only deciduous-hardwood associations present in Fanjingshan, and all of the evergreen notophyllous associations present here are made up of evergreen fagaceous trees, with the members of Castanopsis centered lower and those of Quercus centered higher. On the south-facing slopes of the western portion of Fanjingshan, F. longipetiolata scatters within an altitudinal range of 1,400-1,900 m, with an average coverage of ca. 20%. In this zone, the evergreen notophyllous associations ascend to ca. 2,200 m. On the north-facing slopes of the western portion, two beech associations occur within a range of 1,500-1,900 m. The beech trees in the lower portion of this range are F. longipetiolata. They merge into the upper F. lucida association, in which the average coverage of F. lucida is 40-50%. Immediately higher than 1,900 m is the Tsuga longibracteata association. On the south-facing slopes of the eastern portion, the F. lucida association occupies an altitudinal range of 1,100-1,900 m, with an average coverage of ca. 60-70%. Large trees of F. lucida, to 30 m tall and 1.2 m DBH, are found here. Fagus longipetiolata only occasionally occurs from 1,100 to 1,700 m in this zone. Immediately above 1,900 m is the (evergreen) Quercus stewardiana association. On the north-facing slopes of the eastern portion, the F. lucida association is present within a range of 1,300-1,900 m, and the F. engleriana association occurs at least from 1,900 m to 2,000 m. In

this zone, the coverage of F. lucida within its association is no more than 40-65%, with an average value ca. 20-30%. Fagus longipetiolata is even less frequently found here than in the previous zone. An evergreen sclerophyllous (microphyllous) association is present immediately above the F. engleriana association.

In W Hubei (in most cases of this monograph when mentioned, W Hubei actually refers to NW Hubei, as in this case), the comparative ecology of beeches is not easy to work on, chiefly because of the abundant co-occurrence of F. hayatae subsp. pashanica and the frequent taxonomic confusion between it and F. lucida in the literature. For this discussion, the only important literature available for me is Anonymous (1980), on the forest in Shennongjia. (Shennongjia is located in the center of NW Hubei, and is the most famous and the most extensive forest area in W Hubei.) According to this book (p. 23-24, 76-77), F. engleriana and F. lucida are present in Shennongjia. The former is common; occurring on the slopes (particularly those north-facing ones) and ridge-crests from 1,500 m to 2,200-(2,400) m alt.; often mixed with many deciduous hardwoods; capable of forming its own association at localities higher than 1,700 m; and sometimes forming small pure stands. The latter is never abundant when present; not found in the northern and the lofty central portions of Shennongjia; growing on the slopes and ridge-crests from 1,600 m to 2,000 m alt.; and normally mixed with the former and other deciduous hardwoods.

Now the problem is with the identification of F. lucida in NW Hubei. Chang (1966: 122) only cited two collections of F. lucida from NW Hubei. One of them is at my disposal: A. Henry 6793. It is a F.

hayatae subsp. pashanica. A collection cited by him as F. lucida, from an unclear locality in Hubei, is also a F. hayatae subsp. pashanica (W.Y. Chun 4182). The only collection of F. lucida from NW Hubei I have ever seen is from Shennongjia (1980 Sino-Amer W Hubei Exp. 1479), in addition to the few plants of E.H. Wilson 715 (see the typification portion of this subsection). On the other hand, five collections of F. hayatae subsp. pashanica from NW Hubei are available for me. They show a far larger distribution range than F. lucida, and grow within an altitudinal range of about 1,700-2,100-(2,400 ?) m. The one from Shennongjia (1980 Sino-Amer W Hubei Exp. 1485) was collected only six numbers later than the F. lucida collection mentioned immediately above; the elevation (2,050 m) is only 50 m higher.

The mountains in Shennongjia are continuous with those in NE Sichuan (the Dabashan Range; see 3-1-2). The floristic composition and the vegetation of the eastern portion of the Dabashan Range (in NW Hubei) and those of the western portion of the Range (in NE Sichuan) are very similar. However, I have only seen one collection of F. lucida from NE Sichuan: R.P. Farges 1557, Sichuan-Chengkou. None of the collections of F. lucida from Sichuan cited by Chang (1966) is from NE Sichuan. On the other hand, F. hayatae subsp. pashanica is abundant here. Yang (1978) first published this entity as F. pashanica, based on many collections from a region west of Chengkou, in NE Sichuan. According to him, the widely known beech forest in the Dabashan Range in NE Sichuan is chiefly composed of this entity. The locations and the density of the collecting localities of this entity in NE Sichuan, as represented by the collections under my study, however, push me to say

that Yang's statement about the relative abundance of F. hayatae subsp. pashanica is applicable only to the western region of the Sichuan Dabashan Range. In this region, it occurs within an altitudinal range of 1,200-1,900 m; and either grows with F. engleriana and/or other deciduous hardwoods (including F. brevipetiolata), or forms pure stands. It is abundant enough to be among the most important timber species in that region (Yang, 1978).

More details about the interesting distribution pattern of the four major Chinese beeches in the northwestern range of the genus will be offered in 3-4-4. I shall now go back to the comparative ecology of the Chinese beeches. The previous discussion on F. lucida and F. hayatae subsp. pashanica suggests a geographic replacement phenomenon with these two species. Three facts make this geographical replacement more perceivable. First, F. hayatae subsp. pashanica has almost all its populations centered in NW Hubei and NE Sichuan, where F. lucida is evidently rare. Second, the remaining populations of F. hayatae subsp. pashanica are disjunct in Zhejiang, where F. lucida is absent. Third, the ranges of these two taxa are collectively almost equivalent to the range of the whole genus in Mainland China. However, this geographical replacement may not imply an ecological replacement, at least in the sense of the rough and ready regimes based on temperature and growing-season precipitation. [Note that the whole range of beeches in China is within the Caf subtype in Koeppen's superficialized climatic classification.] It may be proper to mention the altitudinal ranges of the four major Chinese beeches in this connection: F. engleriana, (1,000)-1,600-2,200-(2,400) m; F. longipetiolata, (300)-800-1,600-

(2,400) m; F. lucida, (800)-1,200-1,800-(2,000) m; F. hayatae, (900)-1,600-2,000-(2,200) m. [The two central figures without a pair of parentheses indicate the ranges in which the species show optimum growth and abundance and/or those in which the species are present within the sympatric area of at least two species.] Although the altitudinal range of F. hayatae subsp. pashanica is indeed a bit higher than that of F. lucida, a fact that should be borne in mind is that these two taxa can be described as allopatric, and hence the trivial difference in the optimal growing altitude may in itself be irrelevant to the enquiry on the causes accounting for the difference in their distribution or ecology.

The absence of F. lucida from the very moist mountains of Zhejiang and Dabashan Range probably implies a more drought-oriented ecological adaptation of F. lucida, compared with F. engleriana and F. hayatae. The absence of the latter two species in the southwestern range of the genus, where F. lucida and particularly the southern group of F. longipetiolata are well represented, supports this idea. Furthermore, in view of the adequate humidity and precipitation during the growing-season, it appears that the xeromorphic structure of the leaves must reflect the nature of the substrata - limestone soil on the limestones. Since I fail to detect any difference in important taxonomic features between the F. lucida collections from within this region and from outside it, limestone soil cannot in itself be considered to be the controlling factor in the current distribution of F. lucida. It may be noted that the previously discussed Fanjingshan where F. lucida shows excellent growth, has no limestones among its

various soil-forming bedrocks. The difference in the soil pH value seems to make no sense in this discussion, since the soils of the habitats of different beeches in both Shennongjia and Fanjingshan have a pH value within a range from about 4.5 to 7.0.

The distribution and ecology of F. longipetiolata could be further commented on here, following the foregoing discussions about F. lucida. The optimal temperature for F. longipetiolata is definitely lower than those for the other three beeches, as has been stated or implied previously. However, it seems possible that the eastern group of F. longipetiolata is capable of living under a slightly higher growing-season temperature than the other two groups. In northern Guangdong, F. longipetiolata is common at about 700-800 m alt. In the continuous montane region in W and N Fujien, NE Jiangxi, Zhejiang, and S Anhuei, it is common at 700-1,100 m alt. To copy the fieldnotes of a collection from NE Fujien (R.C. Ching 2273): "600-1,200 m; in dense wood of all evergreens; very common; tree, 80 x 18 ft." Based on a plant survey on a nature reserve in W Fujien, Chang (1981; 49) indicated that F. longipetiolata is common and grows well in the forests at elevations higher than 800 m, while F. lucida is less common and occurs only in the dwarf thickets on the ridge-crests, in the reserve. I shall mention in this connection that the most typical individuals of the eastern group of F. longipetiolata are best represented in N Zhejiang and S Anhuei. As a preliminary conclusion, it may be said that the more derived (more similar to F. lucida and F. hayatae in margin, and thinner) leaves of the eastern group reflect an adaptation to the more humid climate of its habitat in this region. On the other hand, the western group of F.

longipetiolata tends to grow well in the evidently higher montane regions which are not very significantly more southern. In E Yunnan, where the most typical individuals of the southern group are centered, the species is common from 1,500 to 2,000 m alt. A single collection records an extension up to 2,400 m alt.: A. Henry 9027. The evidently drier climate in these habitats has most probably influenced the evolution of the trullate, thicker, and sometimes recurved margin of the leaves of F. longipetiolata growing there.

In explaining the complete absence of F. lucida in the western region of Sichuan Dabashan Range and the abundance of F. hayatae subsp. pashanica in the same region, an additional speculative reason could be advanced, since the entire altitudinal range of the latter taxon there, 1,200-1,900 m, is quite alright for the former taxon outside this region. That is, the most probably cooler growing-season temperature of that region reduces the competitive ability of F. lucida, but does not suppress the optimal growth of F. hayatae subsp. pashanica.

To close this lengthy discussion, I here describe F. lucida as a species capable of growing in the Mixed Deciduous Broad-leaved Forest, with some extension into the Mixed Northern Hardwood Forest (both sensu Wolfe, 1979), in terms of its adaptation to the temperature and precipitation of the growing-season; but it most probably deviates into an adaptation to a drier substratum. The comparative ecology of F. engleriana and F. hayatae will be presented in 3-4-4, along with comments on the very complex distribution patterns of F. engleriana, F. longipetiolata, F. lucida, F. chienii, and F. hayatae subsp. pashanica, in Sichuan and W Hubei.

TAXONOMIC REMARKS:

Before discussing the taxonomy of F. lucida, it would be proper to compare the scale-like cupule-appendages of F. lucida and F. japonica. Those typical for F. lucida are larger (in terms of the absolute size), thicker, stouter, densely hairy and hence yellowish/brownish; while those of the typical subspecies of F. japonica are smaller, thinner, inconspicuously hairy, and whitish.

About 15 fruiting collections are available to me. Although this number is small, the localities are rather evenly distributed within the range of the species, and I do not expect a considerable extension of the ranges of variation of the leaves or the cupule/nut complex. However, the variation of the number of the cupule-valves and that of the number of nuts per cupule, of F. lucida, should be emphasized here. There are basically three types of cupule/nut complex present in F. lucida: 4-valves/2-nuts, with the four valves equally developed and the two nuts likewise equally developed; 4-valves/2-nuts, with the each two more adjacent valves connate to various degrees and the size of the two nuts varying from equal to unequal; 3-valves/1-nut, with the three valves equal in size, or one valve larger or even with two prominent tips. For the third configuration, the single nut is not larger than either of the two nuts of the first configuration.

There is only one collection showing the typical intermediate (the second one) configuration of the cupule/nut complex. Among these 15 collections, those with 3-valved cupules and those with 4-valved cupules are better represented than those with both 3-valved and 4-

valved cupules. The only three collections of the latter type are from the classical Metasequoia area (1) and Fanjingshan (2). These two localities (Sichuan/Hubei; NE Gueizhou) are aligned in a north-south line of about 280 km. The collections with 3-valved cupules are from W Sichuan (1), NE Sichuan (1), W Hubei (1), SC Hunan (3), W Jiangxi (2), and W Fujien (1) (and the two cultivated trees in the Arnold Arboretum, most probably both of which are from W Hubei). On the other hand, those with 4-valved cupules are from SE Gueizhou (1), Gueizhou/Guangxi (1), N Guangxi (2), and SW Hunan (1). The regional differentiation in this feature is evident, though the number of fruiting collections is few. That is, the individuals producing only 3-valved cupules form a belt penetrating the northern range of F. lucida, and occupy about half of its range; the individuals producing only 4-valved cupules form a continuous belt all the way through the southern range of the species; whereas the individuals producing both 3-valved and 4-valved cupules are confined to a small region completely encircled by these two belts. At least two points support the validity of this perception. [If the locality (Hunan-Xinning) of the only collection showing the typical intermediate configuration of cupule/nut complex, as mentioned above, is added here, then this small region is extended about 230 km southeastward.] First, there is no geographical overlap between any two regions. Second, in all of the following three cases, in which the existence of a population is respectively implied by two collections, the configurations of the cupule/nut complex of the two collections are the same. First, the two collections were made at the same locality but at elevations of several hundred meters difference (SC Hunan). Second,

they were made at different localities within a very small area (N Guangxi). Third, both conditions were fulfilled (NE Gueizhou).

However, because I cannot find any geographical differentiation in leaves although the leaves vary greatly, I cannot subdivide F. lucida based only on the geographical differentiation in the cupule/nut complex as stated above. The lucky thing with this taxonomic analysis is, there exists a rather clear geographical correlation with the evolution of the cupule/nut complex in F. lucida. The geographical direction of the differential distribution of the more derived states is from south to north. To offer more information about the evolution of F. lucida, I am happy to discuss the further differentiation of the species within the range of the "3-valved cupule-entity".

The only fruiting collection from W Hubei at my disposal (see above) is that from Shennongjia (1980 Sino-Amer W Hubei Exp. 1479). It has peculiar cupules and atypical leaves. The cupules have a longer and thinner peduncle and very tiny appendages which are spine-like, very thin, very short, and erect on the surface of the cupule-valve; the leaves are broader and thinner than the typical ones of the species. The two cultivated trees in the Arnold Arboretum are more similar in these respects to this Shennongjia collection than to all other collections of the species, both fruiting and sterile ones. One of them (AA-7418 A) was received as a small plant brought back by E. H. Wilson in 1911, with the collection number E.H. Wilson AA-715. On one survey collection of this tree, S. Elsie & S. Erwin (#1953, A) properly indicated: "plant presumably from the type population", and "note the great lag in dates". (The date of E.H. Wilson AA-715 is 1907-5-31.)

The cupules of this tree are very similar to those of the Shennongjia collection, but with a very short peduncle. There is no record of the origin of the other tree (AA-23033-A). However, it is almost beyond doubt that this tree was also brought back by Wilson from the same general region at the same general time, if not exactly the same, judging from the history of collection of Chinese plants and that of the collection and introduction of F. lucida, by foreign botanists. The cupules of this tree are also very similar to those of the Shennongjia collection. In addition, its leaves are so similar to those of the Shennongjia collection that the degree of the trivial difference between them, if claimed, is comparable with the variation between the individuals of a rather homogeneous population. If we consider the aerial distance between Shennongjia and the type locality of the species, Hubei-Xingshan, the amazing and exclusive similarity between the Shennongjia collection and these two cultivated trees becomes not amazing at all. When two plants of a rather wide-ranging species are growing about 50 km apart in an extensive montane region, they might be expected to be very similar.

Chang (1966: 123) described a variety of F. lucida: var. opienica, based on a single collection from W Sichuan (Erbien). Its diagnosis is as follows: "A var. lucida recedit involucris majoribus, bracteis squamiformibus vel sublinguiformibus, adscendentibus vel leviter recurvatis, pedunculis longioribus, circ. 18 mm longis, foliis majoribus.". The type collection is not available to me. Chang & Huang (1988: 116) listed this name as a synonym of F. lucida. They further commented on the infraspecific variation of the cupule features of F.

lucida as follows: "The collections from Hubei and Hunan usually have smaller cupules; have the appendages so tiny as to be inconspicuous so that the surface of the cupule-valves is nearly smooth; and the peduncle is 2-5 mm long. With regard to the collections from other provinces, most of them have appendages scale-like, tightly appressed on the surface of the cupule-valves but with a tiny and acute (cuspidate) apex; and have a peduncle 5-15 mm long, or even up to 18 mm long (var. opienica)." (translation mine). Although I do not know how many collections from Hubei and Hunan backed Chang & Huang's comments, at least they have taken note of the evolution of cupule-appendages of F. lucida in NW Hubei, as I am here discussing. Returning to the variety opienica, however, the original description reminds me of F. chienii. Because I consider this variety to be probably conspecific with F. chienii, more discussion will be offered in 3-4-3.

Chang (1966: 123-124, pl. 20) published a species F. nayonica, based on a single collection from W Gueizhou (Nayong). Its diagnosis is as follows: "Affinis F. lucidae Rehd. et Wils. a qua foliis ellipticis, involucris infra valvas usque ad basin in stipitem obconicum solidum circ. 7 mm longum attenuatis, differt." Chang & Huang (1988: 116) listed this species as a synonym of F. lucida. Unfortunately, I have had no chance to examine the type collection of F. nayonica. A nut shown in the plate associated with the original description has clear, though not at all broad, wings along the three nut-angles. Winged nuts are not seen in F. lucida. Its elliptic to slightly ovate leaves, as described and shown in the line-drawing, are rare in F. lucida. Both of these two peculiarities are characteristic to F. chienii, in addition to

its larger cupules (16-18 mm long). Its unusual cupules with an abruptly constricted lower portion are unlike those of any other beech I have seen. This sort of cupule is not rare in some other fagaceous genera, such as Lithocarpus and Quercus. This plant could be the only representative of the genus Fagus in exhibiting this parallel development. It may be that this collection should be considered to represent a distinct species, but I am reluctant to do so without seeing the type.

Plants of F. lucida with a 3-valves/1-nut configuration of the cupule/nut complex and very tiny and erect cupule-appendages deserve further discussion. They form the northern frontier of F. lucida in NW Hubei, and simultaneously form the northern limit of the northern group of the species. Such a distribution pattern immediately reminds me of the peculiar short-peduncled entity, "yunnanica", of F. longipetiolata, in the southernmost margin of the southern group of the species. In the case of F. longipetiolata, the extension into the drier habitat, which is supposedly the driest one inhabited by any Chinese beech, is associated with the evolution of the leaves, but the ancestral short cupule-peduncle was retained. On the other hand, the extension of some populations of F. lucida into a more humid region seems to go along with a great but seemingly non-adaptive change of the cupule-appendages, in addition to the adaptive evolution of the leaves. Another two interesting contrasts between the major infraspecific differentiation of these two species could be mentioned here. First, the differentiation of the three major groups in F. longipetiolata is chiefly based on the evolution of leaves, whereas that in F. lucida is chiefly based on the evolution of the cupule/nut complex. Second, the evolution of the

leaves in the former case is associated with the environmental adaptation of the whole individual to a considerable extent, whereas the evolution of the cupule/nut complex in the latter case is hard to be interpreted in terms of adaptation.

3-4-3 FAGUS CHIENTII CHENG

Fagus chientii Cheng, (1935 June), Contr. Biol. Lab., Sci. Soc. China,

Bot. Ser. 10: 70-71. [HOLOTYPE: W.C. Cheng 2903, PE, n.v.; ISOTYPES:

A!, E!, IBSC-54558 !, MICH!, US-1626932 !]

DECIDUOUS TREE; 25 m x 95 cm. CURRENT-YEAR SHOOTS lightly colored, yellowish; hairy. BUDS narrowly ovoid. LEAVES elliptic to narrowly ovate. APEX with a short and broad tip. BASE cuneate to rounded. UPPER SURFACE dark green. LOWER SURFACE light green. SECONDARIES 10-12; always terminating in a tooth-tip. Primary/secondary POCKET-DOMATIA present. MARGIN denticulate, always with small but evident teeth. SINUSES convex. PETIOLE 1/8-1/10 as long as the leaf-blade.

CUPULE-PEDUNCLE ca. 1 cm long; similar to the current-year shoots except thinner. The four CUPULE-VALVES narrowly ovate to elliptic, with a rounded apex; ca. 1.2 cm long. CUPULE-APPENDAGES subulate; ca. 2 mm long; recurved. The two NUTS slightly winged along the entire length of the nut-angle; slightly exserted from the cupule-valves. CHINA.

Based on five sheets of the type collection and the original

description.

HOLOTYPE:

W.C. Cheng 2903, CHINA, Sichuan-Pingwu; PE, n.v.; ISOTYPES: A!, E!,
IBSC-54558 !, MICH!, US-1626932 !

The specific epithet is to honor CHIEN Chung-Shu, the leader of
the first generation of Euramerican botany in China.

ILLUSTRATIONS:

None.

DISTRIBUTION AND ECOLOGY:

Aside from the type collection in 1931, no collections of Chinese
beeches have been identified as this species by any worker. The only
description of the habitat of the type tree is "open country, at 1,300 m
alt.". Pingwu is located west of the Dabashan Range in N Sichuan. No
later collections of beeches were made within the territory of Pingwu,
but some beeches were later found in the vicinity. Yang (1978) cited a
collection of F. hayatae subsp. pashanica from Qingchuan, the Xien
(county) immediately east of Pingwu. Two collections of F.
longipetiolata available for me are from Pingwu/Qingchuan and from
Songpan, the Xien immediately west of Pingwu. Based on the type
collection, the only thing to say about the ecology of F. chienii is
that its ecological amplitude would not be very distant from the norm
for F. lucida.

The nearest localities of F. lucida, the closest relative of F.

chienii, are about 350 km to the south (Erbien and Shimien, in W Sichuan), and about 350 km to the east (Chengkou, in NE Sichuan). It is notable that the west-east line connecting Songpan, Pingwu, and Qingchuan is just the northern limit of the Chinese beeches in their most northwest range. It is most probably the increasing continentality of the climate that checks the northward extension of beeches.

TAXONOMIC REMARKS:

Cheng (1935: 70) indicated that "This very distinct species is apparently related to Fagus longipetiolata Seem. and F. lucida Rehd. & Wils.." He said that "Its leaves with a pubescence on the lower surface and involucre with subulate, recurved scales show clearly its relationship to F. longipetiolata, ..." This statement is very misleading. The pubescence referred to by Cheng consists of long hairs persistent on the major veins, and the only cupule-appendages approaching "subulate and recurved" in appearance are those of F. bijiensis, which was collected and described about 30 years later and whose appendages are most properly described as linear, rather than subulate. Cheng, however, enumerated many similarities between F. lucida and F. chienii in both leaves and cupule-appendages, before he correctly wrote: "... deduce to its origin from F. lucida.". Chang & Huang (1988: 116) suspected F. chienii to be a variant of F. lucida.

In my opinion, F. chienii, F. lucida, and F. nayonica form a related trio. Such a relationship is comparable with that among F. okamotoi, F. japonica, and F. engleriana. Within each of these two trios, each of the two small species clearly represents an early

offshoot of its respective lineage, and has developed its own autapomorphies.

The woody, stout, subulate, and recurved cupule-appendages of F. chieni can be readily perceived as derived from the woody, stout, short, appressed, and scale-like ones of F. lucida, if the high-degree and exclusive similarity in leaves between these two species is taken into consideration. This situation is comparable with that of F. longipetiolata and F. bijiensis, if the polarity of the evolution of the cupule-appendages were reversed.

The 4-valves/2-nuts configuration (the first type; see 3-4-2) of the cupule/nut complex of F. chieni makes the taxonomic distinction between F. chieni and F. lucida greater. As has mentioned in 3-4-2, the only fruiting collection of F. lucida in NE Sichuan is of 3-valves/1-nut type - this is just the collection of F. lucida whose locality is closest to that of F. chieni to the east. Similarly, the only fruiting collection of F. lucida in W Sichuan (Shimien) is also of this type, and its locality is closest to that of F. chieni to the south. The nearest locality of the "4-valves/2-nut entity" of F. lucida is about 800 km away from Pingwu. The geographical direction of the evolution of F. lucida and the well isolated location of F. chieni from even the range of the most derived group of F. lucida collectively ensure F. chieni to be a good species, in addition to its unique winged nuts and the subulate and recurved cupule-appendages.

The leaves of F. chieni differ a little bit from the more typical leaves of F. lucida in three points: more elliptic and never trullate; with a shorter and broader apex; and more inconspicuous teeth

and less sharply defined tooth-tips. All these three changes can be found individually in the collections of F. lucida in various degrees, but among the specimens of the series Lucidae under my study, the type tree of F. chienii is the only individual that combines all of them.

The taxonomic situation of the variety opienica of F. lucida has been discussed in 3-4-2. Among the five traits of this variety listed by Chang (1966), four are compatible with the concept of F. chienii. They are: the larger cupules, scale-like/sublingulate cupule-appendages which are erect to slightly recurved, and the larger leaves. The last one is the longer cupule-peduncle. The range of variation of the peduncle length of F. lucida as defined here is from 0 to 14 mm; and that of F. chienii is 12-18 mm. The 18 mm-long peduncle of this plant is still allright for F. chienii. However, I will not list this name as a synonym of F. chienii before I see the type, because of the tremendous plasticity of the plants of the series Lucidae. If this plant is considered as conspecific with F. chienii, then the range of F. chienii becomes a nearly north-south trended line of about 350 km long. Moreover, this line almost approaches the western limit of the Chinese beeches (see 3-4-2).

3-4-4 FAGUS HAYATAE PALIBIN

Fagus hayatae Palibin, (1911 June), in Hayata, B., J. Coll. Sci., Imp. Univ. Tokyo 30(1): 286-287. [HOLOTYPE: N. Konoshi (1906-2), TI, (Photo)!]

Fagus sylvatica L. var. ? Hayata, (1908 July), J. Coll. Sci., Imp. Univ.
Tokyo 25(19): 206. [Cited Collection: N. Konishi (1906-2)]

Fagus hayatae Palibin subsp. pashanica (C.C. Yang) Shen, comb. nov.

Fagus pashanica C.C. Yang, (1978 Nov), Acta Phytotax. Sin. 16: 100-101.

[HOLOTYPE: C.C. Yang 75-011, The First Forest Survey Team of Sichuan
(Chengdu)!, ISOTYPES: FSIB!, PE!]

Fagus hayatae Palibin var. zhejiangensis M.C. Liu & M.H. Wu,

in Y.T. Chang & Huang, (1988), Acta Phytotax. Sin. 26: 115.

[HOLOTYPE: M.H. Wu 619, FSIB!; ISOTYPE: ZJFC!]

DECIDUOUS TREES; to 25 m tall and 1 m DBH. BARK whitish; smooth.
CURRENT-YEAR SHOOTS light-colored, yellowish/brownish. BUDS ovoid; to
3-5 mm long by the end of the growing-season. LEAVES trullate to
broadly lanceolate to ovate in subsp. hayatae, elliptic to oblong in
subsp. pashanica; (2)-3-4-(5) cm long in subsp. hayatae, (3)-4-6-(8) cm
in subsp. pashanica; thick-chartaceous. APEX acuminate. BASE cuneate
to (rounded). UPPER SURFACE dark green. LOWER SURFACE light green.
SECONDARIES (8)-10-12-(14); always terminating in a tooth-tip.
Primary/secondary POCKET DOMATIA present. MARGIN denticulate to
(slightly serrate) in subsp. hayatae, serrate to slightly serrate to
(denticulate) in subsp. pashanica. SINUSES convex to sinuous to
(slightly concave) in subsp. hayatae, concave to sinuous when present in
subsp. pashanica. PETIOLE ca. (1/6)-1/8-(1/10) as long as the leaf-
blade.

The flowers per MALE INFLORESCENCE 7-15. The hairs on the upper

portion of the PERIANTH-TUBE eglandular, yellowish. FRUIT MATURING in early August. CUPULE-PEDUNCLE 5-12 mm long in subsp. hayatae, 10-20 mm long in subsp. pashanica; normally thinner than 1 mm; normally hairy. CUPULE-VALVES very small, ca. 7-10 mm long; elliptic, with a rounded apex. CUPULE-APPENDAGES linear; ca. 2-3 mm long; recurved. NUTS always very prominently winged; always well exserted from the cupule-valves. CHINA. Two subspecies recognized.

HOLOTYPE OF SUBSP. HAYATAE:

N. Konishi (1906-2), CHINA, Taiwan-Taipei; TI (Photo)!

The specific (and subspecific) epithet is to honor HAYATA Bunzo, the most eminent Japanese plant taxonomist of the flora of Taiwan.

HOLOTYPE OF SUBSP. PASHANICA:

C.C. Yang 75-011, CHINA, Sichuan-Nanjiang; The First Forest Survey Team of Sichuan (Chengdu)!; ISOTYPES: As Above!, FSIB!, PE!

The word "pashan" refers to the Dabashan Range. Extensive populations of this entity occur in the NE Sichuan portion of the Dabashan.

ILLUSTRATIONS:

Subsp. hayatae: T.S. Liu (1960: 600); Lin & T. Liu (1965: Fig. 1); Liao (1971: 109); T.S. Liu & Liao (1976: 77); etc.

Subsp. pashanica: Yang (1978: Fig. 1).

DISTRIBUTION AND ECOLOGY:

The subspecies hayatae is restricted to N Taiwan. The subspecies

pashanica is disjunct in Zhejiang and in the Dabashan Range of W Hubei and NE Sichuan. N Taiwan is the southeastern limit of the Chinese (and East Asian) beeches. Zhejiang is almost the northeastern limit of the Chinese beeches. The Dabashan Range is the northwestern limit of the extensive populations of the Chinese beeches.

For the whole species, the vast majority of the populations is located in the Dabashan. The distribution and ecology of these populations have been discussed in 3-4-2. Additional information is offered here, particularly about the relative distribution and comparative ecology of F. engleriana (of the subgenus Engleriana) and F. hayatae (of the subgenus Fagus).

I shall begin the discussion with an introduction of the geography and topography of my subject region. Within the territory of Hubei, beeches are found only in the western portion - the montane area of the Sheng (Province). Within the territory of Sichuan, conterminous to Hubei to its west, beeches grow in the mountains surrounding the Sichuan Basin. The mountains are continuous about the boundary between Hubei and Sichuan. The Dabashan Range trends east-west, and is broad and long, though not very lofty. In the broadest sense of its name, the Dabashan forms the northern boundary of the Sichuan Basin, and occupies almost the whole NW Hubei (north of the Changjiang [=Yangtze River]).

Fagus longipetiolata most probably originated as a northern subtropical element (see 3-3-2 and 3-4-2). It extends northward into a cooler climatic regime in the form of its northern group, and seems to be checked along the line connecting Changyang, Badong, Wushan, Wuxi, and Chengkou, from east to west. In Hubei, this line is immediately

south of and almost parallels Changjiang. Along this line, the species seems not exceed 1,600 m alt. Fagus lucida would have a more northern extension in this region, in the form of its "3-valves/1-nut entity", judging from the comparative ecology of it and F. longipetiolata. This is true. Its northern limit is a line connecting Shennongjia and Chengkou. Fagus longipetiolata never goes into the Dabashan, whereas F. lucida occurs on the southern side of the major divide of the Hubei Dabashan (see 3-4-2).

[Chang (1966: 118) cited two collections of F. longipetiolata from Shaanxi-Pingli, which is on the northern side of the major divide of the Dabashan and is not very far from Hubei-Fang and Sichuan-Chengkou in aerial distance. They could be regarded as representing "relic" population(s) of F. longipetiolata since the "hypsithermal" (= xerothermic) period of the current Interglacial. Chang (1966: 122) cited a collection of F. lucida from Hubei-Fang. It is unavailable to me, and I am uneasy about the identification because all sterile collections showing similarities to both F. lucida and F. hayatae subsp. pashanica would have been identified as F. lucida at that time.]

F. hayatae subsp. pashanica seems to be restricted within the Hubei Dabashan, and the western portion of the Sichuan Dabashan, in this region. It seems never to be in contact with F. longipetiolata, because all of the clear localities of F. hayatae in Hubei are in Hubei Dabashan (Ichang, Xingshan, Shennongjia, and Fang; from south to north), and at elevations from 1,700 m to 2,200 m. The Fang locality (A. Henry 6793) is on the northern side of the major divide of the Hubei Dabashan. Although the collections of F. hayatae and those of F. lucida from the

Hubei Dabashan at my disposal are few, the ratio of five to two in favor of F. hayatae implies the relative abundance of F. hayatae over F. lucida in Hubei Dabashan. However, the most abundant beech in the Hubei Dabashan is undoubtedly F. engleriana, and there F. hayatae and F. lucida are collectively described as "not abundant" (both see 3-4-2). The much better adaptation of F. engleriana to the colder climatic regime than F. hayatae subsp. pashanica is well evidenced in the Hubei Dabashan. About 200 km to the north, a single record of F. engleriana is made in Henan-Lushi (ca. 34 degrees N).

No collections of F. hayatae from the most northeastern portion of the Sichuan Dabashan are available to me. On the other hand, F. engleriana is abundant here (Wushan, Wushi, Chengkou, and Wanyuen; from east to west). In fact, the range of F. engleriana is continuous from the Hubei Dabashan to the most important distribution area of F. hayatae in the western portion of the Sichuan Dabashan. Immediately west of Wanyuen, in Tongjiang and Nanjiang, F. hayatae subsp. pashanica occurs within an altitudinal range of 1,200-1,900 m. At higher elevations within this range, it becomes abundant. Further to the west, the westernmost locality of F. hayatae subsp. pashanica is in Qingchuan. At the proper elevations in the general area of Tongjiang and Nanjiang, this taxon seems to flourish to an extent comparable with what F. engleriana achieves in the proper habitats in the Hubei Dabashan. In this connection, I must question why no collections of F. hayatae subsp. pashanica from the general region embracing Wushan, Wushi, Chengkou, and Wanyuen are available for me. According to E. H. Wilson's travel route, the localities in NE Sichuan where F. lucida (for them, a concept

combining F. lucida and F. hayatae subsp. pashanica) was said to be "fairly common" (Rehder & Wilson, 1916: 192) should be around Wushan and Wushi. I here suppose a relatively quantitative distribution pattern for F. engleriana and F. hayatae subsp. pashanica as follows: along the entire Dabashan Range, the continuously distributed F. hayatae subsp. pashanica obtains its optimal habitats in the lower mountains in the west, whereas F. engleriana enjoys its optimal habitats in the higher mountains in the east.

In Nanjiang, F. engleriana often mixes with F. hayatae in the same stand (Yang, 1978). These stands can sometimes extend far down to ca. 1,200 m alt. (J.W. Ge Nanjiang-1 Population) - the lower limit for F. hayatae. With the increasing elevation, the importance of F. hayatae increases significantly, but that of F. engleriana does not. On the other hand, F. engleriana displays its cold-adaptation in its appearance on the south-facing slopes of Qinling Range in Shaanxi (Liouba, Chenggu, Hanyin, Pingli, and Danfeng; from west to east). One of its two northernmost locality in Shaanxi is in Danfeng, which is conterminous with Henan-Lushi, and at ca. 33.5 degrees N. Its westernmost locality in Shaanxi, Liouba, is located almost straight north of Sichuan-Nanjiang. Fagus hayatae has not been found in Shaanxi.

The occurrence of F. engleriana at very low elevations in Nanjiang is perhaps explainable through the very favorable high moisture there. Another notable fact to mention here is the co-occurrence of F. brevipetiolata, F. hayatae, and F. engleriana in a mixed hardwood stand in Nanjiang (J.W. Ge Nanjiang-2 Population, 1,450 m alt.). The nearest locality of F. brevipetiolata is in Hubei-Badong (part of the following

three collections: E.H. Wilson AA-493; AA-700-A; AA-700-B), so far as I know. Other localities of F. brevipetiolata, based on the collections available for me, are in the classical Metasequoia area, C Gueizhou, SE Yunnan, N Guangdong. Chang (1966: 120) cited collections from another two localities in S Sichuan and SC Hunan, respectively. This is the only Chinese beech showing a discrete distribution in a large area in the form of small populations. This distribution pattern may suggest that F. brevipetiolata had flourished at an earlier time, probably no later than the Pliocene.

Now I begin discussing the distribution of the Chinese beeches along their "common" western limit (see 3-4-2). The term "W Sichuan" is here used to denote the geographically central Sichuan according to the current boundary, because the traditional provincial boundary, which is based on the concept of the Sichuan Basin, is far more proper for the researches of natural history. Furthermore, W Sichuan (in this sense), W Gueizhou, and SE Yunnan are geographically and topographically transitional between the western Qinghai-Xizang Plateau and the eastern plain/hill region. This roughly north-south line is one of the primary and the sharpest natural boundaries of the Chinese flora and fauna. The distributions of two major species F. longipetiolata and F. lucida along this line have been stated before. F. engleriana is common from Sichuan-Guan southward to the area approximating the boundary with Yunnan. This is probably the second most important area for this species in terms of the large concentration of its populations. I would further stress the unrivaled significance of this north-south distribution line for the Chinese beeches by stating a simple fact.

That is: five beech names were and are still based on single collections (or two collections from the same locality) along this line: F. chienii (NW Sichuan), F. lucida var. opienica (SW Sichuan), F. bijiensis (NW Gueizhou), F. nayonica (NW Gueizhou), and F. clavata (SW Gueizhou). The name F. longipetiolata forma yunnanica was based on the collections from SE Yunnan, northernmost Vietnam, and westernmost Guangxi, when published. As to the eastern center of the Chinese beeches, it has only offered plants for two names: F. tientaiensis (based on a single tree till now) and F. hayatae var. zhejiangensis. The northern center has only produced one name: F. pashanica. The present monograph does not alter this picture significantly.

In Zhejiang, F. hayatae subsp. pashanica is presently only found on a single mountain (Sihaishan) in Yongjia of S Zhejiang. The altitudinal range of the subspecies is from 850 m to 1,000 m. Direct information about its ecology is so far unavailable. In the extensive montane region in S Zhejiang, vegetation at a similar elevation is basically a notophyllous evergreen broad-leaved forest. The evergreen Fagaceae are invariably the dominant trees in this region. Above about 800 m alt., some non-pioneer deciduous hardwoods are found scattered in the evergreen forest, such as F. longipetiolata. In this connection, it is curious that no collection of F. longipetiolata from Yongjia or its conterminous Xiens (= counties) is at my disposal. If this indeed reflects the reality, then a geographical or an ecological replacement may exist between F. hayatae subsp. pashanica and F. longipetiolata (see 3-4-2; for the case of F. lucida and F. hayatae subsp. pashanica). A further comparison between these two cases seems to lack sufficient

conditions at least for two reasons. First, the relative distribution and ecology of these two species in S Zhejiang are not yet sufficiently known to allow such a comparison. Second, the apparently relic status of F. hayatae subsp. pashanica in S Zhejiang renders this taxon an improper subject for this kind of comparison.

Fagus hayatae subsp. hayatae is confined to N Taiwan. It shows a "relic" distribution pattern there. Its classical and major range (ca. 24.5-25 degrees N) extends about 18 km from north to south, around Takaishan (N Chatianshan). Hsieh (1989: Fig. 2) provided a detailed distribution map of this region. Within this area, F. hayatae subsp. hayatae occurs in relatively pure stands along ridge-crests at elevations of about 1,350-1,950 m. In the lower northern portion, it mingles with subtropical evergreen hardwood species; whereas in the higher southern portion, warm-temperate conifers, such as Chamaecyparis and Tsuga, are among the dominant trees of the mixed transitional forest. In this general region, "The ridges and summits are always wrapped by clouds even in rainless days." (Hsieh, 1989: 29). The soils of the beech forest are well drained, strongly acidic (pH 3.2-4.2), and with a depth varying from 50 to 80 cm.. Outside this area, a single collection has been made in the mountains several tens of kilometers to the east, in Ilan (Suzuki-Tokio 5960).

The population analysis of the beech forests conducted by Hsieh (1989) revealed three interesting points that are useful for my investigation here. First, beeches in the southernmost and highest locality (Lalashan, 1,900-2,000 m) are on the average far taller and stouter than those in the northern and lower localities. Second, the

correlation coefficient between age and DBH of the Lalashan population is significantly greater than that of other populations. Third, on the other hand, old trees are far better represented in the other populations (to 300 years old). These three facts can be used to formulate some inferences about the comparative ecology of F. hayatae subsp. hayatae, along with some vegetational, geographic, topographic, and meteorological facts or estimates, as follows:

First, the large trees (to 17 m tall, 70 cm DBH) of the Lalashan population represent the observable best growth of F. hayatae subsp. hayatae. Second, therefore, the individual habitat conditions in the Lalashan locality should be not very far from the optimal portion of the corresponding ecological amplitudes of this subspecies. Third, the temperature and precipitation of the growing-season in the Lalashan locality of F. hayatae subsp. hayatae would not significantly differ from those in the optimum habitat of F. hayatae subsp. pashanica in the Sichuan Dabashan Range. Fourth, the smaller but older trees of F. hayatae subsp. hayatae in the northern and lower localities can be explained by the limited water-supply during the growing-season. The ridges in this region are strongly wind-swept almost year-round: frequent typhoons in summer and strong northeastern monsoons in winter. The shallow soil (ca. 50 cm thick) on the narrow and steep ridge-crest can hardly supply extra water for beeches to produce more photosynthates than they need to maintain their yearly leafing and mast-year seeding, after the great loss of water through evapotranspiration. Fifth, F. hayatae subsp. hayatae seems to be rather shade-intolerant, based on the following two observations: 1) the absence of beech seedlings and

saplings under the closed canopy of beech stands (Liu & Su, 1972), and 2) the rather stable and constant diameter-growth pattern shown by the large individuals (Hsieh, 1989). Sixth, the predominance of F. hayatae subsp. hayatae in these ridge-crest forests in N Taiwan may be chiefly attributable to the exclusive capability of this beech in thriving and regeneration there, among the trees growing in that general region. Seventh, the weak shade-tolerance of this beech does not seem to affect appreciably the persistence of its populations in their current habitats in N Taiwan. Eighth, along with the slow-growing habit, the weak shade-tolerance, on the other hand, seems very likely to have something to do with the absence of this subspecies elsewhere in Taiwan, and the "relic" situation of this subspecies compared with the other subspecies. Ninth, since all other beech taxa can be described as slow-growing and shade-tolerant, F. hayatae subsp. hayatae, as a gross morphologically derived beech, probably offers a mirror through which the senescent process of a beech is observable. Tenth, the scattered populations of F. lucida on the ridge-crests in WC Fujien (Chang, 1981; see 3-4-2) are probably also characterized by weak shade-tolerance. They are within the geographic range of the 4-valves/2-nuts group of F. lucida, and form the eastern limit of the species. If the roughly continuous populations of F. lucida in Sichuan, Gueizhou, Guangxi, and Hunan were not present for some reason, then the overall situation and the fate of these WC Fujien populations of F. lucida might be similar to those of the populations of F. hayatae subsp. hayatae in N Taiwan.

Both Peters (1988) and Hsieh (1989) noted the similarity among beech forests in Mainland China, Taiwan, and Japan, in the constant

presence of a dense dwarf bamboo understory. The Korean beech forest in Ulreung-Do is also so characterized (Yim, 1983). The taxonomy and autecology of these East Asian dwarf bamboos are more complicated than those of the East Asian beeches. The ancestors of these bamboos and beeches are found together in some Upper Miocene (Uemura, 1988), Pliocene (Koiwai, 1915), and Pleistocene (Onoe, 1989) fossil assemblages. Taxonomic, distributional, and ecological studies on these dwarf bamboos would be very helpful in our understanding of the East Asian beeches. Unfortunately, no updated and comprehensive studies in these respects are currently available for reference.

TAXONOMIC REMARKS:

The populations of the subspecies hayatae in N Taiwan show a reasonable degree of variation in leaves, if one considers the geographic and ecological range of this subspecies there. On the other hand, the cupule/nut complex has very limited variation both within populations and among populations. This variation pattern also characterizes the populations of the subspecies pashanica in the Dabashan Range. The extreme and exclusive similarity in the cupule/nut complex of these two entities warrants the combination of the two specific names F. hayatae and F. pashanica. The leaves of these two entities are sometimes similar, but in most cases they are distinct enough to be considered as representing two subspecies.

Yang (1978) described F. pashanica on the basis of nine collections from Nanjiang (8) and Qingchuan (1), both in the western portion of the Sichuan Dabashan. I examined all of them about three

years ago in Sichuan-Chengdu. Their leaves are consimilar, and are concordant with Yang's description and line-drawing. From this region, another four collections (Nanjiang, 3; Tongjiang, 1), in addition to two isotypes, are at my disposal. Two of these three collections from Nanjiang are population collections. Five collections from the Hubei Dabashan are available to me.

Among these ten collections under my intensive study, only three (C.C. Yang 75-011, Sichuan-Nanjiang; J.W. Ge Nanjiang Population-1; 1980 Sino-Amer W Hubei Exp. 1485) have their cupule/nut complexes mature enough to show the diagnostic traits. The only difference I can find between the "infructescences" of F. hayatae (in N Taiwan) and those of F. pashanica (in NE Sichuan and NW Hubei) is in the length of their peduncles. The cupule-peduncle of F. hayatae is normally 5-10 mm long; whereas that of F. pashanica is 8-15 mm long. The ranges of variation of the various features of cupule/nut complex are very narrow in both taxa. A combined description of the cupule/nut complex will be no different from the individual descriptions of these two taxa. And I cannot at all identify any pair of isolated "infructescence" composed of a F. hayatae and a F. pashanica, without reference of the length of the peduncle. Yang (1978) correctly considered F. hayatae to be close to his F. pashanica, and pertinently mentioned the longer peduncle of F. pashanica in his list of the differences between them, except those in the leaves. Within Fagus, at least four features of the cupule/nut complex may mark species or even subspecies. Since there is simply no way to distinguish the cupule/nut complexes of the plants growing in N Taiwan and in NE Sichuan-NW Hubei respectively, these two specific names

should be combined.

Shen & Boufford (1988) reidentified a collection from Hubei-Shennongjia (fruiting, cited above; originally identified as F. lucida) as F. hayatae. About one year later, I had access to the type and other collections of F. pashanica. Subsequently I found it necessary to recognize only one species composed of two subspecies, and then reassign the Shennongjia collection to F. hayatae subsp. pashanica, based on leaf features.

In comparison, the leaves of the Taiwan plants are generally very small, mostly trullate to ovate, and with the both sides of a tooth roughly equally long and then the tooth more wide spreading; while those of the Central China plants are generally larger, mostly oblong to elliptic, and with the upper side of a tooth shorter than the lower one so that the tooth points forward. In terms of the general shape, it is clear that the gravitational center and the broadest portion are lower in the former than in the latter. The Shennongjia collection is the most atypical one for the subspecies pashanica among my research materials, in both leaf and "infructescence" features. It has a short cupule-peduncle, hence its "infructescences" are not different at all from those of Taiwan plants. Its leaves are similar to those of a few Taiwan plants in size, and are similar to those of typical Taiwan plants in leaf-margin. The only trait on which I rely in my determination of the subspecific assignment of this Shennongjia collection is its mostly oblong leaves. The basic leaf-shape of this individual is not found in any collection of F. hayatae from Taiwan. Concomitantly and/or simultaneously, I place more weight on the basic leaf-shape in

differentiating the two subspecies. Another fact supports this consideration, that is, in a few cases in which the leaves of F. lucida are similar to those of F. hayatae, it is the basic leaf-shape that provides the most reliable distinction.

As has been mentioned previously, the two series Lucidae and Hayatae are closely related, as can be well perceived from the overall similarity in their leaves. This similarity, along with some other gross vegetative features, has led to the admixture of F. lucida and F. hayatae subsp. pashanica in the sterile type collection of F. lucida. It has also caused the misidentifications of all of the sterile collections of F. hayatae from Hubei and Sichuan, and even some fruiting ones (such as that Shennongjia collection), at least before the publication of the name F. pashanica.

The leaves of F. lucida, F. chienii, F. hayatae subsp. pashanica, and F. hayatae subsp. hayatae form an excellent quartet. There is no linear relationship among them. If their "infructescences" were similar, then a well defined species composed of three (or four, but the single representative of F. chienii should be less weighed in this consideration, although it is rather isolated geographically) subspecies would be a satisfactory taxonomy for them. The leaves of these four taxa are collectively characterized, and thus distinguishable from all other living beeches, by the following traits: thick-chartaceous; generally varying from (long) trullate, to (long) ovate, elliptic, and oblong; generally acuminate apex; generally broadly cuneate to rounded base, with the basal margin straight to slightly convex and without teeth; secondaries (8)-10-12-(15) (depending on the length of the leaf-

blade), each of them terminating in a generally sharply defined tooth, which is often ortho-triangular; sinuses often conspicuously convex, but varying to slightly convex or even simply slightly sinuous; petiole generally $(1/6)-1/8-(1/10)$ as long as the leaf-blade.

The leaves of F. hayatae subsp. pashanica have the following four characteristics. First, they mostly vary from oblong to elliptic, seldom ovate, and never exactly trullate. This trait is shared with F. chienii. Second, the broadest portion of many oblong leaves is at the upper side of the geometric rectangle, rather than expressed as a line-segment of the vertical side of the geometric rectangle. This trait is also seen in some leaves of the five isotypes of F. chienii at my disposal, and clearly represents a derived state. Third, when oblong, their basal margin is often a straight line, with the line connecting the two lowermost teeth (on one side each) forming exactly the lower side of the geometric rectangle. The trullate and ovate leaves of many F. hayatae subsp. hayatae and a few F. lucida also have a straight basal margin, and have the line connecting the two lowermost teeth exactly at the broadest portion of the leaf-blade. The derived status of such a basal margin is clear. Fourth, the sinuses are sometimes absent; thus the lower side of a tooth is nearly a geometric line or even a slightly convex line, and it then connects directly with the upper side of the subadjacent tooth. This trait is unique even within the whole genus.

On the other hand, the leaves of F. lucida can be characterized by the following four traits. First, they are mostly long-ovate, but are seldom oblong, elliptic, or trullate. Second, they always have clearly defined teeth, which are often narrowly triangular and directed

upward or even incurved. This trait is only approached by a few collections of F. hayatae subsp. hayatae, and should be considered as an apomorphy within the genus. Third, their apex is always acuminate, and the leaf-blade above the uppermost tooth on each side (defined as the "acme" here) is mostly a very narrow triangle with its two lateral sides approximating geometric lines. Such an acme is approached by F. hayatae. Fourth, their basal margin is mostly slightly convex, and the line connecting the two lowermost teeth (on one side each) is mostly somewhat below the broadest portion of the leaf-blade. This trait is shared with F. chienii, and is clearly plesiomorphic for the group embracing these two series.

The characteristics of the leaves of F. hayatae subsp. hayatae also deserve a separate discussion. They are very small, with the largest ones only similar to the smallest ones of F. lucida in size. [This situation is comparable with those of the sizes of the cupule and of the nuts.] They mostly vary from ovate to trullate, but sometimes approximate elliptic. While only a narrow range of variation of the appearance of leaf-margin bridges over F. lucida and F. hayatae subsp. pashanica, it can be said that about half of the variants of the leaf-margin of F. hayatae subsp. hayatae are compatible with those of F. lucida, whereas the other half can find their counterparts in F. hayatae subsp. pashanica.

As a competent member of the quartet, F. chienii has a distinct position in leaf features, although it is only represented by a single individual. Its leaves are as large as the larger leaves of F. lucida. Its basic leaf-shape is the same as that of F. hayatae subsp. pashanica,

as mentioned before. The appearance of its leaf-margin is closer to the overlapping portion between those of the two subspecies of F. hayatae, than to that between F. lucida and F. hayatae subsp. pashanica. Its base is similar to that of the vast majority of F. lucida. The only unique trait (among the four taxa under comparison) possessed by the leaves of F. chienii is their broadly triangular acme, each of whose two sides is a sigmoid curve. Such a leaf-acme is not found in any specimens of the other three taxa, and is only seen in very occasional specimens of a few other beeches in my experience. Consequently, there seems no strong need to discount the taxonomic significance of such a leaf-acme of F. chienii, although only one collection is represented here.

[The feature of the acme of a leaf-blade is rarely applied in plant taxonomy. It indeed very seldom express itself as an outstanding feature. Nevertheless, I can give an example to demonstrate its usefulness, based on my own experience on the Fagaceae. In my revision of the Fagaceae in Taiwan (Shen, 1984: 54), Quercus globosa was found to be closely related to Q. glauca. Both species are well represented in Taiwan. Among the differentiating features, leaf-acme is prominent. The leaf-acme of Q. glauca is narrowly triangular, with its two sides straight or slightly concave. Such an acme is ordinarily seen in the subgenus Cyclobalanopsis (to which these two species belong) of Quercus in Taiwan. On the other hand, the acme of Q. globosa is definitely broader, and its two sides are constantly strongly-deflexed sigmoid.]

Now I am able to characterize the leaf features of a hypothetical ancestor of the four recognized taxa of the series Lucidae and Hayatae.

Such an ancestral leaf would be about 6-8 cm long, (similar to those typical for F. hayatae subsp. pashanica and F. lucida in length); thus having about 10-12 secondaries; ovate, (similar to some F. hayatae subsp. hayatae and some F. lucida); acuminate in apex; slightly convex in basal margin, (as in the vast majority of F. lucida); having the line connecting the two lowermost teeth (on one side each) slightly lower than the broadest portion of the leaf-blade, (as in the vast majority of F. lucida); having clearly discernible and slightly uppointed teeth, which are triangular and with the lower side at most slightly longer than the upper side, (similar to those typical for F. hayatae subsp. hayatae); and having sinuses varying from slightly sinuous to slightly convex (as those typical for F. hayatae subsp. hayatae). Such a leaf is certainly not present in F. chienii, but can be found in individual leaves of the other three taxa.

The cupule of F. hayatae looks like a miniature of the cupule of F. longipetiolata, but its appendages are shorter relative to the size of the cupule-valves. The relative length of the peduncle to the cupule-valves is similar in F. hayatae subsp. hayatae and the vast majority of the collections of F. lucida; whereas this value is similar in F. hayatae subsp. pashanica and the collections of F. lucida from the Dabashan Range (see 3-4-2). In this connection, the evolutionary change of the peduncle-length in Fagus merits some comments. When used with a range of variation, the length of cupule-peduncle serves as a rather good diagnostic feature at the specific and subspecific levels within the genus. The evolutionary polarity of this feature can be determined through the following considerations. First, the cupule of the genus

Fagus is supposed to have formed by two 3-valved/1-nutted primitive "flower-cupules" on a reduced peduncle of the partial-inflorescences (Shen, unpubl. ms, 1991 July). A distally aborted peduncle with only two small cupules would not have been as long as 7 cm. Second, the long peduncles of the taxa of the subgenus Engleriana and morphologically typical F. longipetiolata invariably (the former) or often (the latter) show a thinner middle portion, and are pendulous at full maturity. This phenomenon suggests an originally shorter (and stouter) peduncle. Third, the peduncles (= fructescence) of all other fagaceous genera are woody and straight when the fruit(s) is/are mature, and at least somewhat stouter than those of Fagus. These facts imply a primitively stouter cupule-peduncle for Fagus.

Two respects of evolutionary changes are discussed here together: that in the size of the cupule-valves, and that in the relative length of cupule-valves to the included nuts, because both of these two respects are seen very close to one end of the respective continuum in F. hayatae. The primitiveness of the small and thin cupule-valves within the genus seems to be beyond dispute. The polarity of the latter feature is not easy to determine, for at least two reasons. First, the length of cupule-valves and that of nuts are two different features. These two organs have no inherent reasons to change their length in the same direction and at the same speed (absolute or relative). Hence, it is very likely that this "evolution" is eventually a "pseudo-evolution", although this feature is taxonomically useful. Second, I observe no adaptational advantage in any variant of this feature over others. And the supposition of a relatively faster evolutionary speed of the

elongation of cupule-valves, to offer a better protection for the developing nuts, is theoretically untenable because the cupule-valves of beeches are distinct throughout ontogeny, and is practically also untenable because the diagnostic cupule/nut complex of a taxon is observable almost immediately after pollination. However, some clues in this regard are likely to obtain through a detailed discussion on the relevant taxa.

In most species and subspecies of Fagus, the nuts are roughly level with the cupule-valves. The only case in which the nuts are appreciably lower than the cupule-valves is found in a few collections of F. engleriana. In contrast, the nuts are normally well exserted from the valves in F. japonica, F. hayatae, and F. grandifolia subsp. grandifolia, and most F. lucida. Particularly in F. japonica, nuts that are only half covered by the valves are frequently seen. It is notable that both of the only two taxa that have scale-like cupule-appendages and definitely wingless nuts, F. japonica subsp. japonica and F. lucida, have their nuts exserted.

That the scale-like appendages of these two taxa are primitive and are not secondarily derived within the genus is clear for two reasons. The first one invokes the overall evolution of the cupule-appendages of the whole family (Shen, unpubl., 1991 July; and 3-1-3). The second one is stated as follows. The various "intermediate" (between scale-like and linear) cupule-appendages as seen in some small species and subspecies can be grouped into two categories. The first category is composed of the appendages of F. chienii and F. bijiensis (if applicable); and the second one incorporates those of F. japonica

subsp. angustifolia, F. okamotoi, and the unnamed entity of F. lucida in the Dabashan Range. The appendages of the first category are really somewhere around the middle portion of the morphological continuum connecting triangular scales and long and recurved lines, hence they cannot be used as a direct reference for the determination of polarity. On the contrary, those of the second category unambiguously and powerfully support the genuinely symplesiomorphic status of the appendages of F. japonica subsp. japonica and most F. lucida, for the following two reasons. First, at least two kinds of appendages are distinguishable within this category, and morphologically both of them are apparently closer to scales than to linear/cylindric structures. Second, this morphological connection is concordant with the taxonomic affinity of the plants involved, it hence represents a genuine morphological evolution.

It is clear that the presence of the primitively scale-like cupule-appendages on the primitively small cupule-valves of F. japonica subsp. japonica cannot imply the primitiveness of the very well exerted nuts of this taxon, relative to all other taxa. The consubgeneric F. okamotoi has roughly equally small cupule-valves that are roughly level with the prominently winged nuts. The third species of this subgenus, F. engleriana, has far larger cupule-valves which are either level with or slightly overtopping the nuts that are winged only on the upper portion. Both of the latter two species have specialized, but completely different cupule-appendages. Two conclusions can be drawn now. First, the similar size of the nuts of F. japonica (subsp. japonica) to those of F. engleriana can be added into the picture to

refer to a "rapid" correlated evolution between the size of the cupule-valves, the morphology of the cupule-appendages, and the winged condition of the nuts in the immediate ancestry of F. engleriana. Second, the very small size of the nuts of F. okamotoi is better considered as an apomorphy within the subgenus, along with the very prominent wings of the nuts and the very specialized morphology of the cupule-appendages.

The evolutionary situation of the cupule/nut complex of F. hayatae should be discussed in the context of the subgenus *Fagus*. Leaving F. lucida and F. hayatae aside, the vast majority of the species and subspecies of this subgenus have large (larger than F. lucida) cupule-valves, linear appendages, and somewhat winged nuts that are either level with or slightly exserted from the cupule-valves. The only conclusion I can draw at this moment is: the very small nuts of F. hayatae are better regarded as derived within the subgenus, especially after the similarity in size of the nuts of F. lucida to those of other taxa, and the very prominently winged nuts of F. hayatae are taken into consideration.

Based on these discussions, the cupule/nut complex of the hypothetical common ancestor of these two subgenera would most probably be characterized as follows: cupule-valves thin and small, ca. (6)-8-(10) mm long, (similar in size to those of F. japonica, F. okamotoi, and F. hayatae); cupule-appendages scale-like, (similar to those of F. japonica subsp. japonica and most F. lucida); nuts small, ca. 8-10 mm high, (similar in size to those of F. grandifolia subsp. caroliniana), wingless (as those of F. japonica subsp. japonica and F. lucida), and

slightly but generally clearly exerted from the cupule-valves. Such a cupule/nut complex is approached by some specimens of F. japonica. If the length of the cupule-peduncle is also considered for a more complete picture of a mature "infructescence", then the very long peduncle of F. japonica makes its producer fail immediately in the contest, and some specimens of F. lucida win instead.

Now that the pertinent (to the evolution of F. hayatae) portions of the stories about leaves and cupule/nut complex have been presented, I shall return to my speculation on the origin of F. hayatae. I perceive a roughly synchronized diminutive evolution between cupule-valves and nuts in the immediate ancestor of F. hayatae, in addition to, or more likely after, the evolution of the linear cupule-appendages and the prominently winged nuts, as well as an initial development of the straight basal margin of the leaf. In the immediate ancestor of the subspecies pashanica, the cupule-peduncle was elongated, and the ranges of variation of the basic leaf-shape and the tooth-shape were moved in new directions. In the other lineage leading to the subspecies hayatae, the leaves were reduced in size, and the range of variation of the basic leaf-shape was moved in another direction. I do not see any adaptive significance of any of these evolutionary changes.

Before closing the taxonomic discussion about F. hayatae, I should consider the isolated population(s) of F. hayatae in S Zhejiang. Liu & Wu (in Chang & Huang, 1988) described a variety zhejiangensis of F. hayatae, on the basis of three collections from the same mount (Sihaishan) in Zhejiang-Yongjia. In addition to these three collections, I examined another two in FJSI in 1988. Currently there is

only one (still another) collection at my disposal. All of these six collections are from Sihaishan. Three of them were recorded to grow at 850 m, 910m, and 1,000 m alt. respectively. Whether all of these six individuals are from a single population or not is not clearly known, although they are very similar to each other. Aside from the length of the peduncle, the cupule/nut complex of these Zhejiang plants is not distinguishable at all from those of the plants in Taiwan and in Hubei and Sichuan. One additional collection is now available. Accordingly, the taxonomic status (within F. hayatae) of the Zhejiang plants can be and should be determined only by the length of their cupule-peduncle and their leaf features.

The lengths of the cupule-peduncles of the four fruiting Zhejiang collections are as follows: ca. 17 mm; 6-15 mm; ((5))-9-13-((17)) mm; 12-15-(18)-((22)) mm. The only five measurements I can obtain from the available fruiting collections of F. hayatae subsp. pashanica in Hubei and Sichuan are: 5-9 mm (type); ca. 5 mm; 5-9 mm; 12 mm; 10-22 mm (population measurement). Yang (1978) considered the 5-12 mm-long cupule-peduncle of the Sichuan collections available to him to be among the differentiating features between F. pashanica and "F. hayatae". Liao (1971: 110) and Liu & Liao (1976: 78) offered a measurement on the plants in Taiwan: 7-9 mm. My own measurement on the Taiwan plants is ((2))-4-8-((11)). Now the picture becomes more complete and unambiguous, and three conclusions can be drawn. First, the average length of the cupule-peduncle is shortest in the Taiwan plants, and longest in the Zhejiang plants. Second, for the plants in Hubei and Sichuan, about half of the variants of this feature are well within the

range of the Taiwan plants, and the other half are well within the range of the Zhejiang plants. Their far more extensive geographic range and far more flourishing situation readily explain their broader range in this feature. Third, situated at the most specialized end of the continuum of variation of the length of cupule-peduncle, the Zhejiang plants cannot be assigned to F. hayatae subsp. hayatae.

The leaves of the Zhejiang plants are more similar to those of the Central China plants than to the Taiwan plants. They are generally as large as those of the Central China plants, often show the characteristic configuration of tooth/sinus complex of the latter, and have a high (as high as the latter) frequency of occurrence of a straight basal margin. However, three interesting points about the leaves of the Zhejiang plants are notable. First, they are generally ovate or long-ovate; they are never exactly oblong, which is often seen in the Central China plants but is never found in the Taiwan plants; and they are never exactly trullate, which is often found in the Taiwan plants but is never seen in the Central China plants. Second, their petioles are generally longer than the collections of F. hayatae outside Zhejiang. Third, they seem to show a higher frequency of the occurrence of compound teeth than other populations of F. hayatae. Furthermore, the subsidiary teeth are often present on the straight or even slightly convex lower side of a tooth, thus resulting in a unique appearance among beech leaves. All of these similarities and differences in leaves seem to point to a sibling relationship of the Zhejiang plants with the Central China plants. The observations on the length of the cupule-peduncle, as discussed above, are compatible with this perception.

The Zhejiang plants could be considered as representing either a subspecies or a variety of the subspecies pashanica, depending on the taste of taxonomists and/or their personal inclination about the relative importance of cladogenesis and anagenesis. The 900 km aerial distance between Zhejiang-Yongjia and the easternmost locality (in NW Hubei) of the disjunct western range of F. hayatae can support either taxonomic decision in this case. I prefer to take the Zhejiang plants as a variety of the subspecies pashanica. Morphologically speaking, the Zhejiang entity is on the average most specialized among the three entities (at the varietal level) of F. hayatae. On the other hand, the habitats of the Zhejiang entity and of the Taiwan entity may reflect the more specialized temperature adaptation of the Dabashan entity.

To finish the lengthy discussions on the Chinese beeches, I shall draw some conclusions about some of their ecological and gross morphological evolution, the phenetic and evolutionary relationships among them, and the possible selective significance of some taxonomically useful evolutionary changes. First, the ecological evolution of the Chinese beeches is often (phenetically) correlated with gross morphological evolution at the infraspecific or specific levels, as shown by the pair-wise correspondance in the geographic distribution of the features of these two respects individually. This phenomenon is observed in all of the four major species, and it is thus also associated with the taxonomic differentiation at specific (F. engleriana only) or infraspecific levels.

Second, the first members or immediate ancestors of all four major Chinese beech species must have grown in a northern subtropical

climatic regime (of the Northern Hemisphere). The former case is applicable to F. longipetiolata, F. lucida, and F. hayatae; whereas the latter occurs in F. engleriana. [Fagus japonica still has an appreciable part of its ecological range in the northern subtropical regime.] In the cases of F. engleriana and F. lucida, this statement is based chiefly on the distinctive evolution of the cupule/nut complex. On the other hand, this conclusion is a result from the previous lengthy argumentation on F. longipetiolata and F. hayatae.

Third, the expansion of the range of (growing-season) temperature adaptation toward a colder one has evidently occurred during the infraspecific differentiation of F. lucida and F. hayatae, and during the evolution of F. engleriana. This kind of change is most probably chiefly associated with the competitive ability of beeches in summer through photosynthesis. In my study on Chinese beeches, I can detect no traces suggesting a reversed change in the adaptation to the summer temperature. [Non-growing-season temperature, on the other hand, has certainly also been associated with the ecological evolution and the current geographic distribution of beeches, but the adaptation in this respect seems to chiefly improve the cold-tolerance of beeches in harsh winter in terms of survival. Meteorological information pertinent to the study on the cold-tolerance of beeches is so incomplete that I do not think a discussion on this respect is feasible for this monograph. In addition, no direct ecophysiological references on beeches in this respect are known to me. (For information on some other deciduous hardwoods, see e.g., Kaku & Iwaya, 1978; 1979; among others.) However, to account fully for the ecological evolution and distribution of

beeches, information on the winter-temperature adaptation is indispensable.]

Fourth, it seems very likely that the optimal habitat for the immediate ancestor or the first member of at least F. longipetiolata and F. lucida was not as humid as the current habitats of beeches in Dabashan, or in the mountains of Zhejiang or N Taiwan. The growing-season precipitation of such an "ancestral" habitat would be most probably no less than about 1,000 mm/yr. With a high relative humidity (no less than 80-85% all-year-round; for protection of the bark and root-system of beeches from fire), and a well drained substratum that had a reasonably high field-capacity of water, the net water supply would then be enough for these beeches. However, the ecophysiological mechanism of the adaptation or simply tolerance to a very humid habitat of some Chinese beeches (such as those growing at the higher elevations in the Dabashan) is currently unknown.

Fifth, an expansion in the (growing-season) humidity adaptation to cope with a drier substratum must have happened in some populations of F. longipetiolata and F. lucida. Whether a morphological (or physiological, or both) evolution of the root-system has gone along with this adaptational change or not is unclear.

Sixth, no genetic reasons are perceived to have destined the "partnership" between some "covarying" variants of the habitat adaptation and the various "infructescence" features respectively. Some pairs of this kind are present in the infraspecific entities of the species F. longipetiolata, F. lucida, and F. hayatae respectively, and in F. engleriana (in contrast to F. japonica). Some discussions are

necessary to account for the substantial relationship between some gross morphological evolution and the ecological evolution of the Chinese beeches, at least in terms of subspeciation. First, extension in the range of habitat adaptation of a plant species would not by itself immediately and definitely initiate, and finally directly result in a subspeciation. It begins as a kind of commonplace in the results of the genetic behavior at the individual and population levels, and it can thus immediately contribute to the dynamic composition of the local vegetation, sometimes even significantly. However, within a plant species that has reasonably sized ranges in geographic territory and ecological adaptation, this kind of change can hardly lead to a taxonomic differentiation at a higher level, unless it has locally advanced far enough in its ecophysiological attributes, or has caused a large-scale geographic extension of that species. Even so, some level of gross morphological differentiation is necessary to substantiate that taxonomic differentiation. Second, since I see no selective advantage for the more specialized states of all "infructescence" features and some leaf features of at least the Chinese beeches. These morphological traits are probably only randomly fixed. Theoretically, each of them might have gone its own way, independent of geography or ecology. The relative timing of the initiation of these morphological and ecological trends is not pertinent in this connection. Third, perhaps most of these "correlation" phenomena have begun with a certain level of change in the habitat adaptation of the original taxa. After a more extensive geographic range was achieved through a further development of this ecological trend, some (basically) non-selective morphological novelties

would have a higher probability to be randomly fixed in some peripheral populations, through the effect of the marginal population.

Subsequently, the geographic isolation would have sharpened the morphological and ecological distinctions between the isolated populations during the geological period in some cases, to various extents in different features.

Seventh, somewhat unlike the case of the "infructescence", at least two covarying changes in the gross leaf features at about the subspecific level seem to have clear selective significance in some cases. They are the changes in thickness and in general shape. The former is supposedly to have occurred at least in the evolution of the eastern group and the entity "yunnanica" of F. longipetiolata and the NW Hubei plants of F. lucida. The latter is supposed to have been involved in the evolution of the eastern and northern groups of F.

longipetiolata, the NW Hubei plants of F. lucida, and F. hayatae subsp. pashanica. Both of these two evolutionary changes may reflect a change in the humidity of the habitat. However, at least two things in this respect are notable. First, while the changes in the thickness and the general shape of the leaf of a woody dicot taxon are associated with the change in humidity, they sometimes also affect the size of the leaf to some extent. This is just the case of the NW Hubei plants of F. lucida. Second, the environment-associated change in the general shape of the leaf of a woody dicot taxon sometimes goes along with the seemingly non-selective change in some diagnostic or peculiar basic shape of the leaf. This is just the case of the northern group of F. longipetiolata and F. hayatae subsp. pashanica.

Eighth, the evolutionary changes at the subspecific level in the vast majority of the gross leaf features of the Chinese beeches most probably have no genetical or causal relationship with the "corresponding" changes in the habitat adaptation of the plants. Both the pattern and process of this situation are just as discussed in the foregoing sixth conclusion. A similar process is also supposed to have happened in most, if not all, of the applicable patterns with the other useful gross vegetative features at the subspecific level.

Ninth, most probably all of the foregoing eight conclusions are roughly applicable to the specific level, and thus the speciation, of the major Chinese beeches. Moreover, the overall morphological, ecological, and taxonomical picture remains virtually unchanged even when other features are also considered and when all of the small species are added to the list.

Tenth, at the immediately higher level, some other things should be added into the overall picture of the gross morphological evolution, ecological evolution, and the various relationships between them, of the Chinese beeches. Among them, the initial and (basically) spontaneous morphological differentiations which were subsequently strengthened by some large-scale and rapid topomorphological changes had probably played the primary role. At even higher levels, at least the following factor should be considered as relatively more important in causing the current cladogenetic distance as reflected by these taxonomic levels: a very early differentiation in some key morphological feature(s) in a stock species in the geological past.

Finally, the comparison between the leaves of the section

Longipetiolata and those of the subgenus Engleriana is worthy of some comments. The initial gross morphology of the former is supposed as large, ovate, thick-chartaceous, slightly serrate, with specialized eglandular, short hairs on the glaucous lower surface. That of the latter could be most probably characterized as large, slightly obovate, thin-chartaceous, slightly serrate, and with a glaucous lower surface. As has been discussed in 3-3-1, the detailed morphology (under 30 x magnification) of the surface profile that causes the glaucosity is different in these two groups. The waxy nature of the glaucous leaves of the subgenus Engleriana seems to be clear. However, the congested and rather evenly distributed rounded and whitish dots on the lower surface of the leaves of the section Longipetiolata are most probably papillate projections from the epidermal cells. At least the wax-type glaucosity of the lower surface of leaves is frequently considered to have ecological significance in the water budget of the leaves, and the degree of its development is therefore environmentally controlled to some extent, at least at some infraspecific levels. It is possible that the presence of both kinds of glaucosity had indeed affected the overall adaptation of the leaves of the first individuals, and thus the flourishing, of these two groups. As to the possible adaptive advantages these two kinds of glaucosity may contribute to the current representatives of these two groups, a difference may be present. For E. engleriana, its wax-type glaucosity is perhaps not very important, if still important at all, for its current abundance at higher elevations in the Dabashan Range. For the taxa of the section Longipetiolata, their papilla-type glaucosity, if really ecologically significant at

all, may have contributed to their current drier ecological adaptation (and probably also their current broader geographic range) than other Chinese beeches. However, this supposed ecological advantage may not be very outstanding in the chiefly competitive environment of the ordinary current habitats of F. longipetiolata.

3-4-5 FAGUS CRENATA BLUME

Fagus crenata Blume, (1850 Dec), Mus. Bot. Lugd.-Bat. 1: 307. [No collections cited; no figure offered]

Fagus crenata Blume var. procera Blume, (1850 Dec), Mus. Bot. Lugd.-Bat. 1: 307. [No collections cited; no figure offered]

Fagus sieboldii Endl., (1847), Gen. Pl. Suppl. 4(2): 29. [nom. nud.; no collections cited; no figure offered]

Fagus sylvatica L. var. asiatica A.DC. (1864 Nov), Prodr. 16(2): 119. [Collection cited: C. Wilford 1041, G!, GH!, K!, NY!]

Fagus crenata Blume subsp. undulata (Blume) Shen, comb. nov.

Fagus undulatus H.Buerger, in sched., on Buerger s.n. L-16907-77, L!

Fagus crenata Blume var. undulata Blume, (1850 Dec), Mus. Bot. Lugd.-Bat. 1: 307. [No collections cited; no figure offered]

Fagus feruginea ? (non Aiton) Siebold, (1830), Verh. Bat. Gen. Kunsten Wetensch. 12: 25-26. [No description; no collections cited; no figure offered]

Fagus sieboldii Endl. var. undulata (Blume) Miq., (1867), Prol. Fl.

Iap.: 358. [No collections cited; no figure offered.]

DECIDUOUS TREES, to 30 m tall, 1.2 m DBH. BARK smooth, whitish/silvery. CURRENT-YEAR SHOOTS light-colored, yellowish/brownish, sometimes persistently hairy, thick. BUDS sessile, generally cylindric, to 12 mm x 2 mm by the end of the growing-season. LEAVES thick-chartaceous; ovate to nearly trullate or to nearly rhombic (in subsp. crenata), ovate to narrowly ovate or to narrowly elliptic (in subsp. undulata); 6-10-(12) cm long (in subsp. crenata), 3-6-((10)) cm long (in subsp. undulata). APEX (acute) to acuminate (in subsp. crenata), acute to (acuminate) (in subsp. undulata). BASE broadly rounded to broadly cuneate, and often subcordate at the very base (in subsp. crenata), acute to narrowly rounded (in subsp. undulata). UPPER SURFACE dark green. LOWER SURFACE light green; sometimes with persistent whitish long hairs on the major veins. SECONDARIES ((6))-8-10-(12); mostly smoothly upcurved along the crenate margin. Primary/secondary POCKET-DOMATIA always present. MARGIN (slightly sinuous) to slightly crenate to strongly crenate (in subsp. crenata), undulate to slightly sinuous to slightly crenate; minute and triangular teeth seldom present. SINUSES thus mostly absent. PETIOLE ca. 1/8-1/10 as long as the leaf-blade.

Flowers per MALE INFLORESCENCE 15-31. The hairs on the upper portion of the PERIANTH-TUBE glandular, blackish. FRUIT MATURING in July. CUPULE-PEDUNCLE ca. (2)-3-(4) cm long; ca. 1 mm thick. CUPULE-VALVES oblong to elliptic; ca. (10)-15-20-(25) mm long. CUPULE-APPENDAGES generally linear and recurved, the basal ones at least discernibly spatulate-foliaceous, sometimes those on the lower half of

the cupule-valve clearly spatulate-foliaceous. NUTS generally level with the cupule-valves; generally slightly winged along the whole length of the angle. NUT-SCARS triangular. JAPAN.

LECTOTYPIFICATION OF SUBSP. CRENATA:

Siebold s.n. L-16907-74, JAPAN, Honshu-Tochigi; L!

Four early nineteenth-century collections, each represented by one duplicate at my disposal, of this subspecies are reasonable candidates for the lectotype: Siebold s.n. L-16907-74; Siebold s.n. L-16907-70-A; Buerger s.n. L-16907-70-B; and Collector unknown L-16907-75-A. They are supposed to be among the collections that had been examined by Blume while he proposed the names F. crenata and F. crenata var. procera. The first one has a physically attached mature cupule, and is from a clear locality (Tochigi). To it has been affixed a red type label indicating it to be the type of "Fagus crenata Bl.". The remaining three are on the contrary sterile and of unknown origin. This specimen (Siebold s.n. L-16907-74) is also the only one, among the pertinent specimens at my hand, bearing an original identification "Fagus crenata Bl.", most probably by Blume himself. Acceptance of this collection as the lectotype of the subsp. crenata must face the problem that Blume may not have seen any fruiting collection when he proposed all three names in 1850. He did not describe the cupule/nut complex for any of them. However, I here agree that the lectotypification has been properly done by the staff of L. More discussion on this matter will be given subsequently.

The specific epithet refers to the frequently crenate margin of

the leaves. Although a crenate leaf-margin also occurs in F. sylvatica subsp. sylvatica, F. japonica, and F. engleriana, it indeed characterizes this subspecies.

LECTOTYPICATION OF SUBSP. UNDULATA:

Buerger s.n. L-16907-77, JAPAN, Locality unknown; L!

ISO-LECTOTYPES: L-16907-78 !, GH(fragment)!

Among the early nineteenth-century collections of F. crenata I borrowed from L, only three sterile sheets have leaves compatible with the concept of this subspecies. The leaves of one of them are rather typical (Collector unknown, L-16907-76) for the bulk of the plants here considered to belong to this subspecies. It is most probably among the specimens collected and examined by Siebold while he first introduced the Japanese beeches to the western world in a Latin scientific name (as "Fagus feruginea ?"). The vegetative features of the other two sheets are so similar that they can be reasonably expected to be from the same population or even from the same tree (Buerger s.n. L-16907-78; Buerger s.n. L-16907-77). The former specimen was originally identified as "Fagus crenata Bl. Var. undulata", and a red type label has been affixed to it to denote its status as the type of the name "Fagus crenata Bl. var. undulata Miq." by the staff of L. The latter specimen was originally identified as "Fagus undu/atus" by Buerger. The leaves of these two sheets are of a very rare type found perhaps only in the southernmost range of this subspecies. It is not unlikely that the plants producing this rare type of leaves will be someday recognized to be taxonomically different from the bulk of subsp. undulata as defined

here. [For the Japanese botanists, it is this bulk of subsp. undulata (as defined here) that is called F. undulata Buerger ex Miq., when mentioned.] However, it is evident that these two of Buerger specimens are closer to Blume's description of the name F. crenata var. undulata than is Collector unknown L-16907-76.

[At my hand, the only other early nineteenth-century specimen that also has leaves of this rare type is from GH. It was distributed from "Herb. Lugd. Batav.", the herbarium in which all the specimens of F. crenata I borrowed from L were originally deposited. The same person, judging from the same handwriting, pen, and ink, identified this sterile fragment as "Fagus crenata Bl. Var. undulata" on the label accompanying the distribution. The vegetative features of this small branchlet are so similar to those of the two Buerger's sheets that these three branchlets can be expected to be from the same tree. Although the collector of this GH branchlet was not indicated, any and all information points out a simple conclusion: all of these three branchlets collectively represent Buerger's single collection (in 1830-1835).]

Now comes a conceptual (and also technical) problem. That is, on which name I should base the new combination subsp. undulata: F. undulata Buerger ex Miq., or F. crenata var. undulata Blume. Since it is very possible that Buerger's collection is the only and the same one on which Blume had based his name F. crenata var. undulata, and Miquel had based his name F. undulata, the type status of this collection is clear. If Miquel's name was validly published - this is the point I do not know - then I can use Miquel's "holotype" (L-16907-77) as the

lectotype of my combination. Furthermore, this specimen is most probably the only one bearing Buerger's own ink "Fagus undulatus". On the other hand, the specimen L-16907-78 might be the lectotype of my combination, because the associated name F. crenata var. undulata is the first validly published infraspecific name (of F. crenata) for the entity concerned. Japanese botanists have traditionally ascribed the epithet "undulata" to Buerger even though he did not formally publish it. However, I decide to take the most "authentic" specimen as the lectotype of my new combination.

The undulate leaf-margin is atypical for this subspecies, although it is really typical for the type collection. Many leaves of F. sylvatica subsp. orientalis can be described as having an undulate margin. However, in terms of gross morphological evolution, the undulate leaf-margin of the common Japanese beech is modified from a slightly crenate one; whereas that of the Turkish beech is derived from a slightly serrate one. A careful observation on individual leaves may readily prove this point.

ILLUSTRATIONS:

Subsp. crenata: Miyabe & Kudo (1925: Pl. 32); Kurata (1964: Pl. 43); Hayashi (1969: 196-197); Satake et al. (1989: Pl. 78); etc.

Subsp. undulata: none.

DISTRIBUTION AND ECOLOGY:

Fagus crenata is the most important deciduous hardwood species in Japan, both in terms of its broad geographic and altitudinal ranges and

its abundance at so many localities within its range at proper elevations. The title "common Japanese beech" is appropriate for this species. It is estimated to have covered about one third of the territory of Japan before the destruction of its forest by human beings. It is also the most intensively studied Japanese hardwood species in vegetation science and forestry. Its timber is among those most commonly supplied in the market.

Fagus crenata is found throughout the Japanese Archipelago south of about 42.5 degrees N, and is particularly abundant at lower elevations in the northwestern Honshu. [For distribution maps of the species, see Anonymous (1949: Fig. 31), Kurata (1964: 87), and Hayashi (1969: 196), among others.] It forms nearly pure stands close to sea-level at its northern limit in southern Hokkaido. It is curious that F. crenata is still locally an important member in the forest at about 1,000-1,500 m alt. at its southern limit in southern Kyushu. In Honshu, the species occurs from about the sea-level (in northern Honshu) to ca. 2,100 m alt. (in the high mountains in central Honshu). Judging from this peculiar altitudinal adaptation pattern along the roughly north-south oriented Japanese Archipelago, a taxonomically meaningful infraspecific differentiation in temperature adaptation is expected. And the geographic line marking the boundary between these two infraspecific groups most probably connects the south-facing slopes of the high mountains in central Honshu. Such a line is roughly the same line that geographically separates the two subspecies of F. crenata. The two distribution maps that well reflect the relative abundance of the taxa (Anonymous, 1949; Kurara, 1964) could be used to support the

presence and the approximate location of this line.

The geographic range of subsp. undulata is similar to that of F. japonica. This subspecies may be described as a taxon of the Outer Zone of Japan. However, the humidity adaptation of F. japonica and that of F. crenata subsp. undulata are supposed to be different, based on the following three considerations. First, the leaves of these two taxa are very dissimilar in those features that are generally considered to be able to reflect the humidity regime of the habitat, but the leaves of F. japonica and those of F. crenata subsp. crenata are similar in some of these features, such as size and margin. Second, true habitat-sympatry between F. japonica and F. crenata seems to be confined to an area in central Honshu, which is within the southernmost range of F. crenata subsp. crenata and within the northernmost range of F. japonica. The humidity range for optimal growth of the whole species F. japonica (in central Honshu) would not significantly differ from the humidity regime of this habitat-sympatric area. Third, in comparing the leaves of the two subspecies of F. crenata, I find some differences that imply the more xeromorphic nature of the leaves of subsp. undulata, which are smaller but not proportionally thinner. The leaves of a rare type of subsp. undulata, as represented by the type collection of the subspecies, are very narrow and have undulate margins. Another two vegetative characteristics of the subspecies, the normally persistent bud-scales (= stipules) and the proportionally very short petiole, probably have something to do with the adaptation of the subspecies to a drier habitat. [The often persistent bud-scales and the normally very short petiole of Quercus (Cyclobalanopsis) sessilifolia (a species

confined to Japan and Taiwan as currently known) are two outstanding characteristics of the species. They are probably associated with a drier habitat in some manner.]

In all of the Japanese ecological literature available to me, the species F. crenata is discussed as an undivided entity. However, some useful information about the ecology of F. crenata subsp. undulata is extractable from the reports of foreign researchers. The altitudinal range within which subsp. undulata is most abundant is from about 900 m to about 1,600 m. This altitudinal range is roughly applicable to nearly all of the latitudinal profiles throughout the geographic distribution area of subsp. undulata. According to the classification of Hamet-Ahti et al. (1974), the bioclimate of the optimum habitats of subsp. undulata, as described here, is almost exactly their southern orotemperate subzone.

[The bioclimate of the habitats of F. japonica is clearly hemitemperate in the southern range of the species, where the optimal habitats seem to be absent. The optimal habitats of F. japonica, in its northern range, have a southern orotemperate bioclimate. Ecological factors other than temperature regime, such as humidity regime, seem to be more important in controlling the geographic and quantitative distribution of F. japonica, when the situation of F. crenata subsp. undulata is compared.]

The subsp. crenata is far more abundant than the subsp. undulata. It is a typical taxon of the Inner Zone of Japan. Although sometimes it can be found in the Outer Zone of Japan even in considerable abundance, nowhere in the Outer Zone of Japan exists its extensive pure or nearly

pure forest as spectacular as what can be seen in the northern part (north of ca. 36 degrees N) of the Inner Zone of Japan. Roughly speaking, within the geographic range of the Japanese beeches, F. crenata subsp. crenata is most abundant where F. japonica and F. crenata subsp. undulata are not present at all. It is the best representative taxon of the important Japanese montane forest zone "Fagus zone" (= Mixed Northern Hardwood Forest, sensu Wolfe [1979]). In Japan, the middle orotemperate bioclimate of Hamet-Ahti et al. (1974) prevails within this forest belt.

To account for the current northern limit of F. crenata (subsp. crenata), nine hypotheses have been proposed by the Japanese botanists in 1900 (two), 1932, 1938, 1975, 1982, 1985, 1987, and 1988 respectively. The sharp northern limit of F. crenata in the Kuromatsunai Depression of the southwestern peninsula of Hokkaido has caused various opinions on the delimitation of the vegetation zones of Hokkaido. Hamet-Ahti et al. (1974: 71) considered the Kuromatsunai Depression to be "obviously the northern limit of the middle temperate zone." They also regarded the bioclimate of the beech-habitat of some timberlines in N and NW Honshu as upper (= northern) or middle orotemperate. In short, it seems clear that the northern temperate bioclimatic subzone is reached by F. crenata (subsp. crenata), after the back and forth "temperature-training" it experienced at least during the Pleistocene. On the other hand, it is also very likely that F. crenata subsp. undulata has not appreciably deviated from the supposed temperature adaptation of the first members of the species, i.e., southern temperate.

However, change in the humidity adaptation is also important in the evolution of the two subspecies. Both the drought-oriented change in subsp. undulata and the humidity-oriented change in subsp. crenata are evident. In conclusion, F. crenata is the first major beech species so far discussed, whose primary taxonomic subdivision is so elegantly "supported" by the ecological differentiation.

TAXONOMIC REMARKS:

The name F. sieboldii is the first Latin name (in 1847) based on the Japanese beeches. Unfortunately, when he proposed this name, Endlicher only referred to the Japanese plants identified by Siebold as F. ferruginea (now F. grandifolia subsp. grandifolia) in 1830. He provided no description or diagnosis, and cited no collections either. The name F. crenata is the first validly published Latin name (in 1850) based on the Japanese beeches. It was published with two varieties: var. procera and var. undulata. No collections were cited by Blume. Fortunately, seven pertinent sheets are available to me. They are from L, the only herbarium which houses perhaps all of the collections supposed to have been used by Blume while he described these three names. Among these seven early nineteenth-century sheets, however, all of the three most important entities of the Japanese beeches are well represented: F. japonica (2 collections), F. crenata subsp. crenata (4 collections), and F. crenata subsp. undulata (2 collections). The only other specimen at my hand which is also supposed to be among the materials from which Blume described those three names is here considered as a fragment of the type collection of F. crenata var.

undulata.

A further effort to arrange these eight collections correctly under Blume's three names is necessary for nomenclatural purposes. I shall copy the original descriptions of these three names as follows (all measurements have been converted into metric system):

"Fagus crenata Bl.: foliis e basi subrotundata v. subcordata ovatis (4.2-7 cm, 2.5-4.2 cm latis, petiolo 3.2-6.3 mm) obtuse crenatis margine et in venis subtus pubescentibus. - Fagus ferruginea (haud Ait.) Sieb. in Bat. Verh. XII. p. 25. No. 151. - Buna noki s. Kurobuna Japonice. - Cum Varietatibus in Japonia.

Var. procera: foliis majoribus (7-11.4 cm, 3.8-6.4 cm latis, petiolo 4.2-10.5 mm) obtuse crenatis v. repandis.

Var. undulata: foliis minoribus (1.9-5.1 cm, 1.1-2.1 cm latis, petiolo 2.1-3.2 mm) ovatis v. ovato-oblongis obtuse crenatis undulatis."

I think it useful to list the eight pertinent collections (on seven sheets) I borrowed from L, for the convenience of the following discussion:

1. F. japonica (Collector unknown, L-16907-71; sterile), originally identified as "Fagus Sieboldi Endl." by person A.
2. F. japonica (Collector unknown, L-16907-75-A; sterile), originally identified as "Fagus Sieboldi Endl." by person A.
3. F. crenata subsp. crenata (Collector unknown, L-16907-75-B; sterile), originally identified as "Fagus Sieboldi Endl." by person A.
4. F. crenata subsp. crenata (Siebold s.n. L-16907-74; fruiting), originally identified as "F. crenata Bl." by person B.

5. F. crenata subsp. crenata (Siebold s.n. L-16907-70-A; sterile),
originally identified as "F. crenata Bl. Var. procera" by person B.
6. F. crenata subsp. crenata (Buerger s.n. L-16907-70-B; sterile),
originally identified as "F. crenata Bl. Var. procera" by person B.
7. F. crenata subsp. undulata (Collector unknown, L-16907-76; sterile),
originally identified as "Fagus bunanoki" and "F. ferruginea ?"
by person C.
8. F. crenata subsp. undulata (Buerger s.n. L-16907-78; sterile),
originally identified as "F. crenata Bl. Var. undulata" by person
B; (Buerger s.n. L-16907-77; sterile), originally identified as
"Fagus undu/atus" by Buerger, and "Fagus Sieboldi Endl. var.
undulata Miq." by person D.

In this connection, I also think it proper to copy the most important literature on the taxonomy of the Japanese beeches published after 1850, as follows. It is the work of Miquel in 1867 ("Prolusio Florae Iaponicae": 358).

"Fagus Sieboldi ENDL. Gen. pl. Suppl. (F. sylvestris LINN. ex A. GRAY), huc F. crenata BL., cupulae exacte F. sylvaticae. Jeso in montanis SMALL, in m. altis Higo SIEBOLD, in Nippon prov. Senano MAXIM. - var. undulata BL. (F. undulata herb. BUERG.) foliis minoribus firmioribus lucidis diversa."

The "Catalogus Musei Botanici Lugduno-Batavi, Pars Prima, Flora Japonica", published by Miquel in 1870, is useful in checking the specimens at hand. Seven specimens are listed under "Fagus Sieboldi Endl.": K.I. Maximowicz (1), C. Wright (1), H. Buerger (1), P.F. von

Siebold (3), IT00 Keiske (1). Under "Fagus Sieboldi Endl. var. undulata Miq.", there are only two Buerger's specimens. Now some preliminary conclusions can be drawn. First, the latter two of Buerger's specimens most probably represent the single and the only collection on which Blume based his name F. crenata var. undulata. Second, collection No. 7 was most probably made by Siebold. And it should be the best candidate of the "type" of Siebold's identification of the Japanese beeches ("Fagus ferruginea ?" and "Fagus bunanoki" on the sheet; "F. feruginea ?" and "Bunanoki" in the report) in his 1830 report. Third, the Wright collection (s.n., Hokkaido-Hakodate, 1853-1856, sterile) is absent from the specimens I borrowed from L. [Two duplicates of Wright's collection are at hand.] Fourth, collection No. 1 is most probably the one made by IT00 Keiske, because all of the information extractable from the L sheet is clearly suggestive of an early Japanese collector. Fifth, the collector of the collections No. 2 and No. 3 (on the same sheet) seems to be Maximowicz.

Judging from the description of the new specific name F. crenata, it is clear that there were three kinds of plants under the concept of F. crenata in Blume's mind. And he further identified the plants identified by Siebold as F. ferruginea (now F. grandifolia subsp. grandifolia) with the major entity among the three entities he collectively disposed under the name F. crenata. To sort out the collections of the Japanese beeches that are supposed to have been examined by Siebold, those collected by Buerger and Maximowicz should be first put aside. [Siebold finished his manuscript no later than 1829, but Buerger botanized in Japan in 1830-1835, Maximowicz botanized in

Japan in 1860-1866.] Thus, four collections remain. Among these four, three were collected by Siebold himself: No. 4, No. 5, and No. 7. The first two are F. crenata subsp. crenata; the last one is a F. crenata subsp. undulata. Concomitantly, person C should be Siebold.

On the other hand, all of the identifications "Fagus crenata Bl." (No. 4), "Fagus crenata Bl. Var. procera" (No. 5 and No. 6), and "Fagus crenata Bl. Var. undulata" (one sheet of No. 8) were provided by person B. Hence, I have to presume that person B is Blume, although I do not recognize Blume's handwriting. Now the problems are with collections No. 7 and No 4. If No. 7 is indeed among the three Siebold collections listed by Miquel in 1870, then there is no reason to suppose that Blume had not seen it before 1850, when he ascribed Siebold's F. ferruginea to his major entity "F. crenata". [Remember that the No. 7 specimen is most probably the only one bearing Siebold's own ink: "Fagus ferruginea ?".] However, I cannot judge whether any characteristic of subsp. undulata (as defined here; through the collection No. 7) had been intentionally reflected in Blume's description of F. crenata or F. crenata var. procera. Collection No. 4 causes a more serious problem. This L specimen is most probably the only one bearing Blume's own ink: "Fagus crenata Bl.". This is the prime reason why I select it as the type of subsp. crenata. This L specimen best fits the description of Blume's entity F. crenata, among the six collections (= specimens here) of F. crenata studied here. As a result of my analysis, I simply do not know why Blume did not describe the mature cupule attached on the branchlet of this specimen.

Finally, if the person A is Miquel, then the situations of the

collections No. 1, No. 2, and No. 3 immediately become clear. This presumption is also helpful in clarifying the authorship of the name "F. undulata", because the handwriting of person D is very similar to that of person A.

If person B is indeed Blume, then a comparison between his descriptions and the collections examined by him would be productive now. Unfortunately, only one result of this comparison seems to be directly useful in my nomenclature. That is, the collection No. 8 must be among the collections, if there were more than one, on which the name var. undulata was based. The description and the collection fit very well and exclusively in this case, in the leaf-size and leaf-margin. However, the dominant (= general) leaf-shapes of this collection are rhombic and elliptic, rather than "ovate" and "ovato-oblong" as given in the description. The descriptions of the other two Blume's entities F. crenata and F. crenata var. procera are so vague and loose that the remaining seven (at least six of them) collections listed above can fit either of them. As to the specimen best fitting the name itself and the description of F. crenata var. procera, among the four L specimens with Blume's original identifications, No. 6 (identified as "Fagus crenata Bl. Var. procera") wins immediately. Its leaves are typical for the plants entitled (when mentioned) "F. undulata Buerger ex Miq." by contemporary Japanese botanists.

The cupule/nut complex of F. crenata shows a reasonable range of variation, but it is basically similar from the northern to the southern end of the range of the species. On the contrary, the leaves of this species exhibit a gradient-like variation pattern along the north-south

trended geographic range of the species. This gradient has a major "interruption" point in the mountains in C Honshu. Some Japanese plant taxonomists have mentioned the existence of a large-leaved group of F. crenata in its northern range, and a small-leaved group in its southern range, such as Kurata (1964), Hayashi (1969), and Ohba (1989). Nakai published a name var. grandifolia to accommodate the plants with very large leaves in NW Honshu. This name is now chiefly seen on some herbarium sheets, both old and new ones. The plants with smaller leaves in EC and S Honshu, Shikoku, and Kyushu are normally called F. undulata Buerger ex Miq., if mentioned at all, at least in the books and research papers published in Japan after the Second World War.

[The epithet "undulata" originated with Buerger's F. undulatus in sched. Blume used this epithet in his validly published name F. crenata var. undulata in 1850, without mentioning its origin. In 1867 Miquel accepted the name F. sieboldii for all Japanese beeches, and published the name "Fagus Sieboldi Endl. var. undulata Bl." (Miquel cited a collection of Maximowicz for F. sieboldii. I have to presume that this is just the sheet now at L on which both the No. 2 and No. 3 collections are mounted. Thus, F. japonica is represented in his concept of the name F. sieboldii.) Miquel clearly attributed the epithet "undulata" to Buerger. His consistent use of the name "Fagus Sieboldi Endl. var. undulata Miq." in his "Catalogus" (1870: 86) and in his identifications of the specimens in his herbarium clearly reflects his taxonomic viewpoint on this entity. To my limited knowledge, I do not know whether or not Miquel published a name "Fagus undulata Buerger".]

So far as I know, the only contemporary work in which the

southern, small-leaved F. crenata was seriously considered is that of Hayashi (1969: 197). Unfortunately, I do not know if his name "F. crenata Blume var. undulata (Buerger) Hayashi" has been validly published. He mentioned several other diagnostic traits of his variety, in addition to its small leaves, and discussed into details of its geographic distribution. Among these "extra" traits, the usually rather crowded ultimate branchlets is pertinent. This trait is somehow associated with the small leaves in beeches, because a similar appearance is also typical for F. hayatae subsp. hayatae. The only useful differentiating trait of this southern entity, other than its small leaves, is its normally persistent bud-scales (= modified stipules), in my opinion. In the collections of F. crenata at my disposal, I have never seen any collection bearing leaves of the typical size of subsp. crenata that retained its bud-scales, or any collection bearing leaves of the typical size of subsp. undulata but with caducous bud-scales. For the collections from the rather broad transitional belt of the two subspecies, those having larger (than those typical for subsp. undulata) leaves usually do not retain their bud-scales; whereas those having smaller (than those typical for subsp. crenata) leaves usually have persistent bud-scales. Thus, specimens that are really hard to identify to subspecies are not many. This situation is not worse than those of F. sylvatica and F. grandifolia. [Fagus sylvatica is commonly thought (but see 3-5) to be particularly notorious, or famous, for the presence of a very extensive transitional area between its subsp. sylvatica and subsp. orientalis, and a name F. moesiaca has been proposed chiefly for the extensive beech populations thriving in

this area.]

As mentioned before, within the geographic range of subsp. undulata, there are some plants showing a rare type of leaf. The type tree of subsp. undulata is among them. However, to my limited knowledge, there seem no contemporary Japanese plant taxonomists who have mentioned the existence of this sort of leaves in their treatments of the Japanese beeches. There are only four sterile collections bearing this sort of leaves under my study, including the type. Their leaves are usually small, always narrow, always undulate-margined, and usually with a short petiole (relative to leaf-blade). These individuals can be classified as subsp. undulata based on their small leaves, except the collection Collector unknown, US-39348, whose leaves have an average length well fitting the value of subsp. crenata. The general shapes of the leaves of these four collections are just the laterally narrowed ones of the leaves of F. crenata, but it should be noted that the length/width ratio of leaves is significantly different between these four plants and all other collections of F. crenata at hand. The undulate leaf-margin is typical for these four trees, although it is also sometimes seen in the remaining collections of subsp. undulata. However, these three plants are further characterized by small leaves. The localities of two of these three collections are clear: Shikoku (M.Yamanaka s.n., (1957-7-1), TUS-8774) and Kyushu (E.H.Wilson 6240, A).

It is very clear that these four individuals collectively represent an infraspecific entity of F. crenata, and more precisely an entity closer to subsp. undulata than to subsp. crenata. Without

information on cupule/nut complex, a more precise relationship between this entity and the remaining subsp. undulata cannot be deduced. Nevertheless, since I cannot differentiate the two subspecies based on the features of the cupule/nut complex, I do not hold a great hope in finding some taxonomically useful distinctions in these features to further diagnose this entity.

Judging from its leaf features and geographic distribution, this entity could be regarded as representing a further evolution (in leaves) along the way subsp. undulata has developed. The sterile specimens of this entity can be readily sorted out from the piles of beech specimens from throughout the geographic range of the genus, by the shape and margin of their leaves. However, I should mention the possible confusion in this respect between this entity and some members of F. hayatae subsp. hayatae. The leaves of the latter taxon are sometimes only clearly distinguishable from those of this entity by their margin. This fact in itself cannot be used to imply a close relationship between these two entities, because the characteristics of the leaves of these two entities can well be perceived as having different origins in their respective species. Parallelism and/or convergence could explain the similarities between their leaves. The (normal) presence of undulate leaf-margin in F. sylvatica subsp. orientalis should also be similarly explained.

However, I can offer another direction of thinking to explain the similarity between F. hayatae subsp. hayatae and this entity of F. crenata in leaves. That is the possibility of historic hybridization between F. hayatae (subsp. hayatae) and the bulk of F. crenata subsp.

undulata (as defined here). There is no doubt about the land-connection between the Asian continent and the current Japanese Archipelago during some cold periods since the Miocene onward. The northern connection (through the Kuye-Dao [Sakhalin]) is probably more pertinent to this case than is the southern one (through Kyushu). Since F. hayatae subsp. hayatae in N Taiwan is now senescent, the supposition that this entity or its immediate ancestor (still F. hayatae) had thrived in the SE provinces of the Mainland China (such as Fujien, Jiangxi, and Zhejiang) is highly possible. A population of F. hayatae subsp. pashanica grows in S Zhejiang nowadays. In addition, Zhejiang is the province of China that shows the greatest floristic affinity between China and Japan, within the context of the East Asian floristic region. On the side of Japan, the populations of this entity of F. crenata seem to be centered in the southernmost range of the species, i.e., Kyushu and Shikoku. The southernmost populations of F. crenata as so far known, are in the mountains of C Kyushu. The Kyushu collection of this entity under my study, E.H. Wilson 6240, is from these habitats. It may be a valid hypothesis to consider the peculiar traits of this phase of subsp. undulata to reflect genetic interaction following hybridization.

The leaves of F. crenata are highly variable. Some leaves of subsp. crenata are very similar to those of F. japonica, at least superficially. The leaves of the previously discussed entity (of subsp. undulata) are on the other hand very similar to some leaves of F. hayatae subsp. hayatae. Those leaves similar to F. japonica are large, broadly elliptic to nearly rhombic, slightly crenate, thin, and with long, whitish hairs persistent on the major veins or even on the whole

lower surface. They are commonly seen on the individuals growing in NW Honshu, the central area of subsp. crenata, where no F. japonica is found. With a branchlet at hand, however, there will be enough information from the vegetative organs, including that from the leaves themselves, to allow for a correct identification. In this connection, it is interesting to know that the leaves of F. japonica that are most similar to these leaves of F. crenata are just the ones most dissimilar to the leaves of F. engleriana, chiefly because of their crenate margin and their persistent long hairs on the lower surface.

The original general leaf-shape of F. crenata should be broadly ovate. From this shape, the broadly rhombic and broadly elliptic ones developed. I have never seen any collection with exactly oblong leaves. The very narrow shapes are only found in the four collections of the peculiar entity discussed before. The subsp. crenata and the bulk of subsp. undulata are similar in leaf-shape and the relative proportion of the representation of the major leaf-shapes. These facts suggest a highly coherent status of the species F. crenata, even though two subspecies are here recognized. They thus offer an excellent example of an important evolutionary pattern of leaf-shape in the genus Fagus. That is: from ovate to elliptic or rhombic. The route from ovate to elliptic has been observed in the section Longipetiolata (the eastern group of F. longipetiolata and F. tientaiensis), the series Lucidae (the NW Hubei entity of F. lucida and F. chienii), and the series Hayatae (F. hayatae subsp. pashanica, in both Zhejiang and the Dabashan Range). The route from ovate directly to oblong is found in the northern group of F. longipetiolata, some F. lucida, and F. hayatae subsp. pashanica in the

Dabashan. Still another route from ovate directly to trullate is seen in the southern group of F. longipetiolata, some F. lucida, and F. hayatae subsp. hayatae. However, rhombic leaves, as a diagnostic type of a taxon, are only found in F. crenata among the East Asian taxa of the subgenus *Fagus*.

The crenate leaf-margin, as a diagnostic type of leaf-margin, is also only found in F. crenata among the East Asian taxa of the subgenus *Fagus*. Within the whole genus, it is seen elsewhere only in some F. sylvatica subsp. sylvatica and in occasional F. longipetiolata. The vast majority of plants of F. crenata have leaves varying between slightly sinuous, slightly crenate, and strongly crenate. There are a few leaves, in both subspecies, which have discernible small, triangular, blunt-tipped teeth each terminated by a secondary vein, protruding from the slightly sinuous margin. If this kind of leaf is considered as specialized within F. crenata, then one has to explain the origin of at least the slightly crenate margin of the species. If considered in the opposite direction, things become much easier, because this kind of leaf-margin is elsewhere seen in many F. hayatae subsp. hayatae, some F. hayatae subsp. pashanica (in the Dabashan), and a few F. longipetiolata. In F. longipetiolata, I have suggested a derived status for this kind of leaf-margin. In F. hayatae, it should be considered to be very close to the ancestral type of the species. In F. lucida, the evolutionary route which is observable in F. hayatae subsp. hayatae is seen in a further developed condition. Thus, two primary transformation series of the evolution in the leaf-margin of the East Asian taxa of the subgenus *Fagus* could be established. The "major" one

is perceivable in the following series of taxa: F. longipetiolata, F. hayatae (subsp. hayatae), F. lucida; and the "minor" one in F. longipetiolata, F. crenata.

The analysis of leaves presented above strongly suggests two things. First, the leaves of F. crenata are morphologically specialized, and evolutionarily rather isolated. Second, the section Longipetiolata is cladistically not very far from the section Lucida. And the characteristics I have proposed for the primitive leaves of the former would be also applicable to the ancestry of the latter, except the eglandular, short hairs on the glaucous lower leaf-surface.

The cupule/nut complex of F. crenata is similar to that of F. longipetiolata. The only significant difference in this respect resides in the presence of spathulate-foliateous cupule-appendages in F. crenata. A careful examination of the specimens of F. crenata at my disposal shows that every cupule has at least a few basal appendages that qualify as spathulate-foliateous. The cupules of a few collections are even completely covered by spathulate-foliateous appendages. Within the overall evolutionary context of the East Asian taxa of the subgenus *Fagus*, these spathulate-foliateous cupule-appendages undoubtedly represent an autapomorphy of F. crenata. They were derived from the long-linear and hairy ones similar to those of F. longipetiolata, as clearly evidenced by the normal presence of this kind of "primitive" appendages on the upper portion of the same cupule-valve. However, no regional differentiation in the various features of the cupule/nut complex was detected, hence no information on this respect is useful in supporting the infraspecific differentiation based on leaves.

Within the subgenus *Fagus*, the spathulate-foliaceous cupule-appendages are found elsewhere in many *F. sylvatica* and a few collections of each of the three subspecies of *F. grandifolia*, based on my study. In the latter half of the nineteenth-century, many important authors had grouped the common Japanese beech and the Turkish beech into a single taxon, either a variety (of *F. sylvatica*) or a species (*F. sieboldii*), chiefly due to the similarity between their spathulate-foliaceous cupule-appendages. The evolutionary and phylogenetic significance of this similarity will be discussed in 3-5.

3-5 SECTIONS OF THE SUBGENUS FAGUS: SECTION FAGUS

A diagnosis of this section within the subgenus has been offered in the synoptical key to subgenera and sections (see 2-3). A synoptical key to the subspecies of the single species of this section: *F. sylvatica*, is given as follows.

1A. At least the lower CUPULE-APPENDAGES prominently spathulate-foliaceous, the upper ones often also like so. LEAVES relatively thicker; obovate, slightly obovate, or narrowly elliptic. APEX acute; ACME acute to blunt. BASE generally narrowly cuneate, with the basal margin usually straight. MARGIN generally slightly undulate to slightly sinuous. SECONDARIES 8-12. (Current-year shoots), (cupule-peduncles), upper margin of the bud-scales, petioles, leaf-margin, and the major veins on the lower leaf-surface always densely hairy.

CURRENT-YEAR SHOOTS generally rather short (and with medium-sized leaves). **TURKEY** (in both Asia and Europe).

3-5b F. sylvatica subsp. orientalis

1B. The basalmost **CUPULE-APPENDAGES** at most discernibly (= very slightly) spatulate-follicaceous, the upper ones always linear (= thread-like). **LEAVES** relatively thinner. E or W of Turkey.

2A. **LEAVES** generally relatively larger, (8)-10-15-(17) cm long; most often nearly rhombic, sometimes nearly obtrullate or elliptic/rhombic. **APEX** acuminate to (acute); **ACME** acute to acuminate. **BASE** generally cuneate, with the basal margin varying from slightly convex to straight to slightly concave; the very base generally slightly cordate. **MARGIN** generally slightly serrate, sometimes serrate or slightly sinuous, rarely slightly crenate. **SINUSES** generally absent. **SECONDARIES** 10-15-(17). (Current-year shoots), cupule-peduncles, upper margin of the bud-scales, petioles, leaf-margin, and the major veins on the lower leaf-surface generally densely hairy. **CURRENT-YEAR SHOOTS** generally very short (and with large leaves). **CAUCASIA & N IRAN.**

3-5c F. sylvatica subsp. hohenackeriana

2B. **LEAVES** generally relatively smaller, (4)-6-10-(14) cm long; most often broadly elliptic/oblong, sometimes nearly orbicular, rarely ovate. **APEX** acute to (blunt); **ACME** acute to blunt. **BASE** cuneate to rounded, but the basal margin rarely concave; the very base never cordate. **MARGIN** slightly serrate, slightly sinuous, or slightly crenate. When slightly serrate, the **SINUSES** slightly

sinuous. **SECONDARIES** (5)-6-10-(12). Cupule-peduncles, upper margin of the bud-scales, petioles, and the major veins on the lower leaf-surface sometimes clearly hairy. The length of the **CURRENT-YEAR SHOOT**s generally similar to those of the beeches in other sections (and with small leaves). **EUROPE**.

3-5a F. sylvatica subsp. sylvatica

Fagus sylvatica L., (1753), Sp. Pl.: 998. [No collections cited; no figure offered]

Fagus sylvatica L. subsp. orientalis (Lipsky) Greuter & Burdet (pro parte), (1981), Willdenowia 11(2): 279.

Fagus sylvatica L. var. asiatica A.DC. (pro parte), (1864 Nov), Prodromus 16-2: 119. [Collections cited: Balansa 130, n.v.; Balansa 1141, A!, G! US-2501971 !; Tchihatch 781, n.v.]

Fagus orientalis Lipsky (pro parte), (1898), Trudy Imp. S.-Peterb. Bot. Sada 14(2): 300-301. [Collections cited: Sintenis 581, G!; Sintenis 5113, A!, G(3)!; others n.v.]

Fagus sylvatica L. subsp. hohenackeriana (Palibin) Shen, comb. nov.

Fagi sylvaticae L. var. macrophylla Hohen. (nomen nudum), (1838), Bull. Soc. Imp. Nat. Mosc. 10(3): 259. [No collections cited; no figure offered]

Fagus sylvatica L. var. macrophylla Hohen. ex A.DC., (1864 Nov), Prodromus 16-2: 118. [No collections cited; no figure offered]

Fagus sylvatica L. var. asiatica A.DC. (pro parte), (1864 Nov),

Prodromus 16-2: 119. [Collection cited: Aucher 5325, G!]

Fagus hohenackeriana Palibin, (1908 May), Bull. Herb. Boiss. 2-8(5):

378. [No collections cited; no figure offered]

LARGE DECIDUOUS TREES, to 40 m tall, 1.5 m DBH. **BARK** smooth; silvery/whitish; densely beset with tiny, rice-grain- to small red-bean-sized, protruded lenticels (in subsp. sylvatica), or with dense, very narrow, vertically aligned fissures of the exploded lenticels (in subsp. hohenackeriana). **CURRENT-YEAR SHOOTS** sometimes (in subsp. orientalis and subsp. hohenackeriana) densely covered by persistent long, whitish hairs, but only very seldom so (in subsp. sylvatica); in almost all cases the glabrescent shoots turning purplish very quickly. **BUDS** fusiform, apex acute; large, to 2 x 0.3 cm (in subsp. hohenackeriana) by the end of the growing-season; the bud-scales always densely hairy on their upper margin (in subsp. orientalis and subsp. hohenackeriana). **LEAVES** broadly elliptic/oblong, sometimes nearly orbicular, rarely ovate (in subsp. sylvatica), obovate to narrowly elliptic (in subsp. orientalis), nearly rhombic, sometimes elliptic/rhombic or nearly obtrullate (in subsp. hohenackeriana); (4)-6-10-(14) cm long in subsp. sylvatica, (6)-8-10-(12) cm long in subsp. orientalis, or (8)-10-15-(17) cm long in subsp. hohenackeriana; thick-chartaceous in subsp. orientalis and some subsp. sylvatica, thin-chartaceous in subsp. hohenackeriana and some subsp. sylvatica. **APEX** acute to acuminate (and ACME acute to blunt) in subsp. sylvatica, generally acute (and ACME acute to blunt) in subsp. orientalis, or acuminate to (acute) (and ACME acute) in subsp. hohenackeriana. **BASE** rounded to cuneate in subsp. sylvatica, generally

narrowly cuneate (and the very base never cordate) in subsp. orientalis, or generally narrowly cuneate (and the very base usually cordate) in subsp. hohenackeriana. UPPER SURFACE often darker green (in subsp. orientalis), often lighter green (in the other two subspecies); generally with persistent hairs on the midrib (in subsp. orientalis and subsp. hohenackeriana). LOWER SURFACE paler than the upper surface; normally with persistent long, whitish hairs on the major veins (in subsp. orientalis and subsp. hohenackeriana). SECONDARIES ((5))-6-10-(12) in subsp. sylvatica, 8-12 in subsp. orientalis, or 10-15-(17) in subsp. hohenackeriana. TERTIARIES nearly always exmedially geniculate (in subsp. sylvatica), often so (in subsp. orientalis), or rarely so (in subsp. hohenackeriana). Primary/secondary POCKET-DOMATIA always present, particularly conspicuous in subsp. orientalis and subsp. hohenackeriana. MARGIN conspicuously ciliate (in subsp. orientalis and subsp. hohenackeriana); slightly crenate to slightly sinuous to slightly serrate (in subsp. sylvatica), slightly undulate to slightly sinuous (in subsp. orientalis), or serrate to slightly serrate to (slightly sinuous) to ((slightly crenate)) (in subsp. hohenackeriana). PETIOLE densely hairy in subsp. orientalis and subsp. hohenackeriana; proportionally longer (ca. 1/6-1/8 as long as the leaf-blade) in subsp. sylvatica and in subsp. orientalis, shorter (ca. 1/8-1/10-[1/12] as long as the leaf-blade) in subsp. hohenackeriana.

The flowers per MALE INFLORESCENCE ca. 15-31-(40). The hairs on the upper portion of the PERIANTH-TUBE often eglandular and whitish (in subsp. sylvatica), often glandular and blackish (in the other two subspecies). FRUIT MATURING in July. CUPULE-PEDUNCLE normally more

than 1 mm thick; ca. (1.5)-2-3-((4)) cm long; generally glabrescent (in subsp. sylvatica), sometimes densely hairy (in the other two subspecies). CUPULE-VALVES generally elliptic; thick; ca. 1.5-2.5 cm long. CUPULE-APPENDAGES normally two types on the same cupule-valve; the linear type ones sometimes slightly recurved, at least present at the top of the cupule-valve (in subsp. orientalis), or nearly covering the whole surface of the cupule-valve (in subsp. sylvatica); the spatulate-foliaceous type ones at least discernible at the very base of the cupule-valve (in subsp. sylvatica), or nearly covering the whole surface of the cupule-valve (in subsp. orientalis). NUTS always prominently winged along the whole length of the angle; normally level with the cupule-valves. NUT-SCARS always sharply triangular. EUROPE (subsp. sylvatica), TURKEY (both European and Asian) (subsp. orientalis), CAUCASIA and N IRAN (subsp. hohenackeriana).

LECTOTYPIFICATION OF SUBSP. SYLVATICA:

The genus Fagus (sensu L.) is represented by four collections in the Linnaean Herbarium (Genus 1130-1, -2, -3, -4). The first two are chestnuts. The third is a sterile collection of F. grandifolia. The final one is a small flowering branchlet of a beech tree. It is pinned on the sheet on which the third collection was mounted. Neither locality nor identification was provided for this flowering branchlet. Although it is likely to be a F. grandifolia, I simply cannot identify it because its leaves are so small and still partially folded.

The common European beech is famous for its natural variation in leaves. There are too many names available for those individuals that

are valuable for cultivation. Other than these, names published for the various populations of the common European beech are also too numerous to be considered one by one. Most of them are based on some trivial differences in color of the bark, size of the leaves, number of the secondary veins, general leaf-shape, leaf-apex, leaf-base, length of the cupule-peduncle, size of the cupule-valves, etc. Furthermore, for the bulk of these named populations, the correlation among their very limited characteristics is either rather weak, or with little taxonomic significance at higher infraspecific levels for beeches. Even sometimes supported by geographic and/or ecological distinctions, at most only a few of these names could be recognized at the varietal level within a species represented only by the common European beech.

Aside from F. sylvatica, the only name that accommodates extensive beech populations in Europe is F. moesiaca. It refers to the beech populations distributed in the southeastern (and eastern) range of the genus Fagus in Europe. The overall similarity and difference between the plants of this entity and those of the Caucasian beech, Turkish beech, and the common European beech growing in W, S, and C Europe might support a roughly subspecific status for this entity. However, this entity represents a complicated (genetic) mixture among the three beech entities surrounding it, in my opinion.

Although broadly recognizable by the general public in W, S, and C Europe, the common European beech exhibits tremendous variation in various gross features, particularly in leaves. Many versions of the taxonomic treatment of the common European beech have been published. Unfortunately, I have not yet found a lectotypification for this entity

at specific or subspecific level. To select a collection or a tree as the "type" of the common European beech seems to be a job more appropriate for my European colleagues than for me.

The original spelling of the epithet "sylvatica" by Linnaeus is retained, although it is a medieval spelling (see the Ex.1 of the Art. 73-1 of the 1988 Code).

LECTOTYPIFICATION OF SUBSP. ORIENTALIS:

P. Sintenis 5113, TURKEY, (A4) Kastamonu; LE n.v.

ISO-LECTOTYPES: A!, G(3)!, US-2501956 !, K n.v. Lectotypified by F. Yaltirik, in 1982, in Flora of Turkey 7: 658, for F. orientalis.

Lipsky cited no less than ten collections when he published the name F. orientalis in 1898, but he did not designate a type. Yaltirik (1982: 658) selected the collection Sintenis 5113 from the syntypes of the name F. orientalis as the "holo." (in LE) of the name F. orientalis. Among the specimens at hand, there are three syntypes of the name F. orientalis, that are congruent with my concept of subsp. orientalis. Among these three, the collection Sintenis 5113 is best represented (by four duplicates). This fruiting collection is rather typical for the taxon in gross morphology, except its extraordinarily long cupule-peduncle. [This trait is reflected by the fact that Haussknecht proposed a herbarium name using the varietal epithet longepedunculata on the labels of these four specimens in 1893.] Very long peduncles are found in occasional collections of all of the three subspecies as defined here, and this trait is not considered to be useful in the taxonomy within these three entities.

Greuter & Burdet (1981: 279) did not do anything other than validly publish their new combination through a journal citation of Lipsky's name. The same combination was also proposed by the Rev. Bjoern Alden, in the same year (1981 Nov), as seen in his annotation labels on many specimens of *G.* In conclusion, I think it proper to accept the lectotype of *F. orientalis*, selected by Yaltirik in 1982, as the lectotype of "*F. sylvatica* L. subsp. *orientalis* (Lipsky) Greuter & Burdet".

LECTOTYPIFICATION OF SUBSP. HOHENACKERIANA:

R.F. Hohenacker s.n., U.S.S.R., AZERBAJDZHAN-Talysh; G! (a branchlet bearing eight leaves and one cupule with a 4 cm-long peduncle)

ISO-LECTOTYPES: E!, G(2)!, LE n.v., US-254305 !.

Palibin (1908: 378) indicated that "typus in Herb. Barbey-Boissier et in Herb. hort. Petropolitani", but did not cite this collection. No information extractable from Palibin's report is useful in tracing the type collection. Whether Palibin had annotated the LE specimens of the type collection or not is unknown to me, although this is very likely.

Among the specimens of the Herbar Barbey-Boissier (now in G) available to me, many belong to this subspecies. Among the latter, there are three sheets (in one collection-folder) collected by Hohenacker. The leaves of these fruiting specimens are very large (11-14 cm long in one specimen). However, they are perhaps from two individuals, as implied by the larger leaves and much longer cupule-peduncle of one of them and the smaller leaves and shorter peduncles of

another two. They are most probably among the plants on which Hohenacker based his name F. sylvatica var. macrophylla. The LE duplicates of these (supposedly) two collections are also very likely the specimens on which Palibin based his new name in honor of R. F. Hohenacker. Therefore, I am very happy to designate a G specimen (the one with eight larger leaves and one cupule with a long peduncle) of this collection as the lectotype of subsp. hohenackeriana.

In the title of Palibin's ad hoc short note describing this new entity, the epithet was printed as "hohenackerana" in boldface. In the text of this note, it was printed as "hohenackeriana", as he consistently spelled it in all his identification labels I have ever seen, and in his unpublished monograph (cited by Czeaczott, 1932). In accordance with the Recomm. 73C-1-(d) of the 1988 Code, the spelling "hohenackeriana" is here adopted.

ILLUSTRATIONS:

Subsp. sylvatica: Tournefort (1700: Pl. 351); Godet (1988: 31); etc.

Subsp. orientalis: Turrill (1930: Pl. 3137); etc.

Subsp. hohenackeriana: none, so far as I know.

DISTRIBUTION AND ECOLOGY:

The common names of the three subspecies defined here should be clarified first. Traditionally, the beech trees growing in Europe are all called the common European beech, whereas those found in and east of Turkey are called Oriental beech. During the first half of the current century, the beech populations growing in the Balkan Peninsula were

intensively studied, and the epithet "moesiaca" was used at various levels to accommodate these populations. These studies were sometimes focused on the supposed hybridization between the common European beech and the Oriental beech, and the geographic delimitation between them, in SE Europe and/or Crimea. In recent literature, the beech populations in Crimea are mostly considered to be of hybrid origin (Fagus x taurica), whereas those in SE Europe are almost universally regarded as a part of the continuous populations of the common European beech, except some populations scattered in the southeastern region of the Balkan Peninsula. The latter are generally considered as of hybrid origin. Simultaneously, the southeasternmost corner of the Balkan Peninsula is included in the geographic range of the Oriental beech.

The "intermediate" beech populations growing in the southernmost Poland, Czechoslovakia, Hungary, and the five Balkan countries, are here considered as belonging to subsp. sylvatica. Hence, the name "common European beech" is to be used here to be equivalent to "F. sylvatica s.s.". Concomitantly, the name "Moesian beech" refers to these "intermediate" populations of F. sylvatica s.s. in SE and E Europe, and the name "typical European beech" will be applied to the extensive populations of F. sylvatica s.s. in W, S, and C Europe.

Traditionally, the name F. orientalis refers to the beeches growing in Turkey, the Caucasia, and N Iran. Unfortunately, probably no information about the taxonomy and geography of subsp. hohenackeriana has been published, since Palibin described this entity in 1908. However, among the Turkish specimens at my hand, I simply cannot find one with leaves typical for subsp. hohenackeriana. On the other hand,

none of the few specimens having many conspicuously spatulate-foliaceous cupule-appendages bears leaves typical for subsp. orientalis. Therefore, subsp. orientalis (as defined here) will be called the "Turkish beech", and subsp. hohenackeriana will be called the "Caucasian beech", in this monograph. When I use the name F. orientalis hereafter, I refer to a combined "entity" of the Turkish beech and the Caucasian beech.

Good maps showing the juxtaposed ranges of F. sylvatica s.s. and F. orientalis are present in Milesescu et al. (1967: 88), Meusel & Jager (1989: 317), etc.. Maps of the range of F. sylvatica s.s. are available in Laemmermayr (1926: Pl. 17), Erdtman (1932: 202), etc.. Maps of the range of F. orientalis have been published by Czeaczott (1932: 387), Browicz & Zielinski (1982: 118), etc. Yaltirik (1982: 887) supplied a dotted distribution map of F. orientalis within the territory of Turkey.

The subspecies sylvatica is distributed in the non-mediterranean and non-continental climatic regions in Europe. In terms of Koeppen's classification, it is confined to Cbf, Caf, and Daf climatic subtypes. A geographically transitional belt between subsp. sylvatica and subsp. orientalis occurs in SE Balkan Peninsula. Some "intermediate" forms are found in this general region. Since some leaves of subsp. sylvatica somewhat resemble those typical for subsp. orientalis, the remarkably spatulate-foliaceous appendages predominant on the cupule-valves of subsp. orientalis undoubtedly become the most reliable trait for a correct identification of the beeches found there. It seems clear that in the sympatric area, the "good" individuals of subsp. sylvatica are mostly found higher than 1,000 m alt; whereas the plants resembling

subsp. orientalis (in vegetative features) tend to grow at relatively lower elevations (see Czechtz, 1932; Alden, 1986; among others).

In this connection, I should mention the distribution and ecology of the Moesian beech. As discussed before, the Moesian beech is abundant in the Balkan Peninsula. To quote Alden (1986: 52): "Forms often called F. moesiaca (K. Maly) Czechtz., with leaves intermediate between the two subspecies, occur throughout the range of ssp. sylvatica, but are particularly frequent where the two subspecies meet, on the Balkan Peninsula and in NW Anatolia." Although neither of the two reports in which the names F. sylvatica var. moesiaca K. Maly, and F. moesiaca (K. Maly) Czechtz. were described is available to me, there must be at least two "subforms" included in Alden's concept of the Moesian beech, judging from his statement as quoted above. Both subforms have generally serrate leaves that are larger and bear more secondary veins than those of the typical common European beech, that are abundant in W, S, and C Europe. The leaves of the first subform are thinner, generally broadly elliptic to sometimes rhombic or nearly orbicular. This kind of leaf characterizes the extensive low-elevational beech populations in SE and E Europe, the scattered beech populations of the so-called moesiaca phase "throughout the range of ssp. sylvatica", some beech populations in the Crimean Peninsula, and some beech populations in the Amanos Mountains of S Turkey. When a local botanist of an E or SE European country mentions the Moesian beech, he mostly refers only to those individuals bearing this kind of leaf. I see no resemblance between the leaves of this first subform of the Moesian beech and those typical for the Turkish beech. The leaves

of the second subform are relatively thicker, generally obovate and with their nearly straight lower margin tapering into a rounded/cordate very-base. This kind of leaf is found in around the Turkey-in-Asia, NW Asia Minor, the Caucasus, Crimea, and the Amanos Mts., in my observation. Four comments on this kind of leaf are necessary. First, such a leaf is similar to a few leaves of the Turkish beech. However, these leaves of subsp. orientalis are generally smaller, narrower, and have less rounded very-base, more obtuse apex, and less serrate margin, than the leaves of this "moesiaca" subform. Second, the Caucasian populations showing leaves of this second "moesiaca" subform are within the geographic range of subsp. hohenackeriana. Their taxonomy and geography have never been clearly mentioned in literature, so far as I know. Third, all of the populations characterized by this second kind of leaf of the Moesian beech (in the concept of some authors) are here regarded as representing infrasubspecific differentiation of subsp. hohenackeriana. For convenience, a temporary epithet "czeczottiana" will be used thereafter to accommodate these populations. Accordingly, the name Moesian beech refers only to the populations with the first kind of leaf as discussed previously. Fourth, Crimea and the Amanos Mts. are the only two places where both Moesian beech and Czechtott's beech are found, other than SE Balkan Peninsula. More comments on the evolution of the leaves of the Moesian beech and the Czechtott's beech will be provided later.

Based on the preliminary understanding on the so-called Moesian beech as presented immediately above, it is clear that in the SE Balkan Peninsula, at least four "entities" occur: typical European beech, the Moesian beech, Czechtott's beech, and the Turkish beech. Among the

collections under my study, only a few show intermediate traits between subsp. sylvatica and subsp. orientalis, and they are thus hard to identify. Fortunately, none of them is from the transitional region of the two subspecies, in SE Balkans (and in NW Asia Minor). In the S Balkan peninsula, subsp. sylvatica occurs from about 700 to 2,050 m alt., whereas subsp. orientalis is found from close to sea-level to 1,100 m alt.. In this connection, the difference between the typical European beech and the Moesian beech in altitudinal distribution in the Balkan Peninsula should be clarified first. Misic (1957) conducted a large-scale statistical study on the variability and ecology of the beech growing in the whole Yugoslavia. He (1957: 164) detected the existence of "an altitudinal ecocline", and "three well marked altitudinal ecotypes ..., linked by successive populations". These three ecotypes are respectively confined to the three altitudinal belts of 200-1,000 m, 1,000-1,400 m, and 1,400-1,800 m. A picture of the typical leaves of these three ecotypes was shown in his Figure 18 (p. 29). The left two of the leaves of the "subalpine" ecotype well qualify for the "normal" leaves of the Moesian beech. Those of the "hilly" ecotype can only be found in the typical European beech. And those of the "mid-montane" ecotype are just intermediate in gross leaf features.

Many studies concerning the intermediate forms and the hybrid populations between F. sylvatica s.s. and subsp. orientalis in SE Balkan Peninsula and NW Asia Minor are available. The fact that no collections from these two places at my disposal are considered to be of hybrid origin does not imply that no "true" hybrids are present there. However, at least five points are clear to me. First, the typical

European beech has very little opportunity to grow with the Turkish beech in the SE Balkan Peninsula, at least because of their difference in altitudinal range. Second, although the Moesian beech has a rather similar altitudinal range to the Turkish beech in this region, they have very little chance to be found growing together in the same habitat, because of their great difference in drought-tolerance. Third, the coexistence of Czeiczott's beech and the Turkish beech is expectable, due to their rough similarity in the adaptation in both temperature and humidity. Fourth, as discussed before, the Czeiczott's beech grows in the low-montane region of E Thrace (in Bulgaria, Greece, and Turkey-in-Europe) and NW Asia Minor, besides Crimea, the Caucasus, and Amanos Mts. Fifth, although Czeiczott's beech is similar to a few Turkish beech in vegetative features, I have not yet found any "intermediate" collection from the both sides of the Sea of Marmara that I cannot identify.

With a preliminary understanding on the horizontal and vertical distribution of the typical European beech and the Moesian beech, now I am able to discuss the ecology of subsp. sylvatica. The populations of the Moesian beech seem to be centered in the mid-montane region of E Europe, such as in the Carpathian Mts. and the Transylvanian Alps. In S and SE Europe, the Moesian beech grows at lower elevations, where it is generally not abundant. It has scattered populations in W and C Europe, where the typical European beech abounds. Within the entire geographic range of subsp. sylvatica, the typical European beech most probably occurs everywhere. It normally grows at higher elevations in the more southern area where the Moesian beech is also properly represented, and on lowlands in the western and northern range of subsp. sylvatica where

the Moesian beech is often absent. The horizontal and vertical gradation between the Moesian beech and the typical European beech is generally paralleled by the gradation in various vegetative features. A SE-NW trend is evident. In this sense, the simultaneous use of the two names "typical European beech" and "Moesian beech", can be regarded as a convenience. On the other hand, the differentiation between these two beeches in ecological amplitude of temperature and humidity can be perceived more clearly through the use of these two names.

The optimal habitats of the typical European beech (in lowlands of W Europe) generally have a slightly lower summer temperature and a slightly higher winter temperature, than the optimal habitats of the Moesian beech (in mountains of E Europe). Thus, the annual range in temperature becomes significantly smaller in the optimal habitats of the typical European beech. On the other hand, the growing-season precipitation is normally slightly higher in the optimal habitats of the Moesian beech. These differences are paralleled by the differential distribution of the natural vegetation. That is, the W European lowlands are well within the range of the deciduous broad-leaved forest, whereas the E European highlands are well covered by the mixed forest made up of evergreen conifers and deciduous hardwoods.

In this connection, another critical issue comes into the picture. According to Koeppen's climatic classification, the prevailing subtypes in the E European highlands are Daf and Dbf, and the W European lowlands are under Cbf subtype, which represents the normal climate in the western margin of the continent in the mid-latitudinal Northern Hemisphere. A similar climatic region (Cbf) in the western margin of

the North American continent fosters a flourishing growth of an evergreen coniferous forest composed of Abies, Picea, Tsuga, Pseudotsuga, Taxus, Thuja, and Chamaecyparis. In the Daf and Dbf climatic regions present elsewhere in the Northern Hemisphere, i.e., in East Asia and E North America, a mixed deciduous hardwood forest (with or without a few pinaceous conifers) is typical. Following a consideration of the major climatic factors and the vegetation of W Europe, W North America, E North America, and East Asia, Wolfe (1979: 27) commented that "Clearly, no present temperature or precipitation factor (or combinations of both) is responsible for the development of broad-leaved deciduous forest in much of Europe." Wolfe (1979: 27) further pointed out that "Europe has almost no mesic areas primarily suited for broad-leaved deciduous forests.", and "It has not been emphasized previously that the nemoral zone of Europe has a temperature regime best suited for a Mixed Coniferous forest;".

I have to try to reconcile the relevant portion of the bioclimatic system of Hamet-Ahti et al. (1974) with Wolfe's (1979) vegetational classification and Koeppen's general climatic system. Simultaneously, I shall try to propose a scheme of the ecological evolution of both deciduous hardwoods and evergreen conifers, before I can go further into the ecology of F. sylvatica subsp. sylvatica. Such a combined effort should be based on East Asia, for two reasons. First, East Asia is the only region in the Northern Hemisphere where a complete series of mesic climatic and vegetational types (from tropical rain forest to taiga) is present, with each type well represented in a broad latitudinal belt and covering an extensive area. Second, Wolfe has

prepared a marvelous chart presenting the "temperature data and classification of humid to mesic forests of eastern Asia, 427 stations" in Plate 2 of his 1979 paper. Again, I find it useful to develop my argument item by item as follows:

First, the various climatic regimes under which non-microphyllous (non-sclerophyllous) evergreen hardwoods thrive are similar in having a coldest month mean temperature very close to or higher than the freezing point, and a warmest month mean temperature higher than ca. 20 degrees.

Second, the various climatic regimes which foster the growth of deciduous hardwoods may be collectively characterized by a coldest month mean temperature very close to or lower than the freezing point, and a warmest month mean temperature higher than ca. 20 degrees.

Third, evergreen conifers are normally found under two kinds of temperature regimes. The first one shows a coldest month mean temperature generally lower than the freezing point, and a warmest month mean temperature lower than ca. 20 degrees. Such a regime fosters optimal growth of various species of Abies, Picea, Tsuga, Pseudotsuga, Taxus, etc. The second one has a very narrow range in coldest month mean temperature from ca. +1 to ca. -1 degrees, and a warmest month mean temperature higher than ca. 20 degrees. Various Northern Hemispheric coniferous genera from various families flourish under such a temperature regime. Naturally, in habitats with a warmer winter, some of these conifers form mixed forest with evergreen hardwoods; otherwise a mixed forest made up of deciduous hardwoods and evergreen conifers occurs.

Fourth, the above ecological characterization of the forests of

(non-sclerophyllous) evergreen hardwoods, (non-pioneer) cold-deciduous hardwoods, and evergreen conifers, in the Northern Hemisphere, may reflect the primary trends of the ecological evolution of deciduous hardwoods and evergreen conifers in the Northern Hemisphere. Discussions in this respect will be presented subsequently.

Fifth, the transitional subzone between the Tropical and Meridional zones of Hamet-Ahti et al., "Subtropical" (= hemimeridional, following their principle of nomenclature), is roughly equivalent to the Paratropical climate of Wolfe. No beeches grow under this climate.

Sixth, the Notophyllous Evergreen Broad-leaved Forest prevails in the "typical" Meridional zone (with three subzones, excl. hemimeridional), and does not grow beyond the hemitemperate subzone. In the low/middle montane region where a cooler oro-Meridional climate prevails, many Northern Hemispheric coniferous genera are well represented, such as (Taxodium), Sequoia, (Glyptostrobus), Cunninghamia, Calocedrus, Amentotaxus, Torreya, Pseudotaxus, etc. Some non-pioneer deciduous hardwood trees are also well represented in, or confined to cooler oro-Meridional climates. Fagus longipetiolata is among the former. However, it should be noted that in this latitudinal belt, a highland climate can hardly have an exact equivalent in lowland.

Seventh, Koeppen's Caf climate is defined to exhibit a coldest month mean temperature higher than the freezing point, and a warmest month mean temperature higher than 22 degrees. Under such a temperature regime, almost no deciduous broad-leaved trees can be found, based on the actual situation as compiled by Wolfe. The Cbf climate differs from the Caf subtype in its lower summer temperature (a warmest month mean

temperature lower than 22 degrees). The appearance of a Cbf climate at proper elevations within this very broad latitudinal belt might be expectable, because of the relatively greater decreasing rate of summer temperature with increasing elevation (compared with the decreasing rate with increasing latitude). Unfortunately, Cbf climatic stations are very poorly represented in Wolfe's chart. Whether this basically reflects the rarity of "true" Cbf climate in E Asia or not is unknown to me. However, three tendencies of ecological evolution might have occurred under a Cbf climate, judging from Wolfe's chart. The first one is the evolution of the hardwoods from an evergreen habit to a deciduous one. The second is that some evergreen conifers had developed into a mixed coniferous forest, and thus had got rid of their previous deciduous-hardwood companions. The third is that some other evergreen conifers had developed into their own (mixed ?, or nearly pure ?) forest, and thus had got rid of their previous evergreen-hardwood companions.

Eighth, the (lowland) hemitemperate subzone is not equivalent to the climate under which the Mixed Mesophytic Forest (MMF) flourishes. As mentioned in the sixth item, the Notophyllous Evergreen Broad-leaved Forest extends well into the (lowland) hemitemperate subzone, and many of its members sometimes intermingle with deciduous broad-leaved trees there. On the other hand, among the common members of the MMF, evergreen broad-leaved species are not numerous, and they are mostly poorly represented in the canopy layer. The East Asian MMF is essentially a deciduous hardwood forest, with evergreen hardwoods and evergreen conifers as accessories. The evergreen conifers are

taxonomically diverse, but quantitatively minor. Wolfe's chart shows that the East Asian MMF is chiefly present under a C/Daf climatic regime, and is sometimes also found in C/D-a/b-f and Da/bf temperature regimes. It would be reasonable to suppose that the C/D-a/b-f MMF has more evergreen broad-leaved members, and in the Da/bf MMF the evergreen conifers are better represented. In East Asia, the deciduous hardwoods are much better represented in the MMF than in any other major forest type, in terms of the numbers of species and genera. Furthermore, in East Asia, the so-called (Northern Hemispheric) relic deciduous hardwood genera are either confined to or chiefly found in MMF. Elsewhere in the Northern Hemisphere, these relic groups are very poorly represented in the MMF of E North America, and are barely present in the MMF of the Caucasia and N Iran. The following coniferous genera are chiefly found in the MMF: Pseudolarix, Pseudotsuga, Keteleeria, (Sciadopitys), Metasequoia, Sequoiadendron, Cryptomeria, Taiwania, Cunninghamia, Chamaecyparis, Fokienia, Cephalotaxus, etc.

Ninth, the evolution of both deciduous hardwoods and evergreen conifers in temperature-adaptation, as could be perceived from Wolfe's Plate 2, now seems to be more clear. It is almost self-evident that the C/Daf climate must have played a primary role in the ecological evolution of the deciduous hardwoods. The freezing point seems to be a threshold for an evergreen hardwood tree to develop a cold-deciduous habit, while its original tree-size is still maintained. Two current phytosociety types contain many deciduous hardwoods that thrive under a temperature regime with a coldest month mean temperature just below the freezing point: 1) the MMF, and 2) the Mixed Evergreen and Deciduous

Broad-leaved Forest. The latter vegetation type is composed of many cold-tolerant evergreen hardwoods and some xeromorphic deciduous hardwoods. No conifers can be seen in such a forest, except some xeromorphic pines. This kind of forest is primarily found in hemitemperate and southern temperate lowlands. The various climates of these habitats collectively show a winter temperature similar to that of the MMF climate, but they have a higher summer temperature that is normal for a subtropical forest. The evergreen elements of such a mixed forest are normally members of some common and widespread genera of the Notophyllous Broad-leaved Forest, and the deciduous elements are either conspecific or congeneric with the "non-relic" deciduous members of the MMF.

Tenth, within the context of the ecological evolution of deciduous hardwoods, two conclusions are reached at this moment. The first is that the current MMF in East Asia would be very close to the primeval forest containing the freshly derived cold-deciduous hardwoods that are the ancestors of the current cold-deciduous hardwoods of the Northern Hemisphere. The second is that the formation of a mixed evergreen and deciduous hardwood forest must have occurred after the MMF had well taken shape in the geological history.

Eleventh, a narrow range of the warmest month mean temperature: 20-22 degrees, seems to represent the ecophysiological divide that has consistently and persistently marked the distinctive ecological adaptation between the hardwoods and the cold-tolerant evergreen conifers (such as those of Abies, Picea, Tsuga, Pseudotsuga, Taxus, etc.). For the pertinent conifers, morphological information from

fossils and living materials convincingly demonstrates two things. The first is that the fossils of the more thermophilic coniferous genera generally antedate those of the more cold-tolerant ones. The second is that the ancestors of the vast majority of the more cold-tolerant evergreen pinaceous conifers were morphologically similar to the more thermophilic living confamilial or congeneric members. Thus, it becomes very clear that the immediate ancestors of these living cold-tolerant conifers had "struggled" to transcend over the threshold of the 20-22 degrees of the warmest month mean temperature in the geological past while their original tree-size was still maintained. In this connection, another phenomenon should also be noted. That is, the evolution of these cold-tolerant (pinaceous) conifers had also been associated with a lower winter temperature. This supports a speculation that the ecological evolution of the Northern Hemispheric conifers in temperature-adaptation is concordant with a roughly synchronic lowering in both summer and winter temperatures, at least before some of them (or their ancestors) entered into the newly appeared colder habitats. Following this idea, the "transformation series" of the temperature adaptation of the Northern Hemispheric (non-pine) conifers would have begun with an Af climate, followed by Caf, through chiefly Ca/bf (and less importantly C/Daf), and ended in Dbf-Dbw, Dcf-Dcw, and Ddw.

Twelfth (and finally), a "transformation series" of the temperature adaptation of the mesic Northern Hemispheric hardwoods would have begun with an Af climate, followed by Caf, through C/Daf, and ended in Daf and Da/bf-Da/bw. In Hamet-Ahti et al.'s terminology, the bioclimatic subzone in which the deciduous hardwoods are well mixed with

the cold-tolerant evergreen pinaceous conifers is the northern temperate subzone. Such a climate could be described as Da/b, using Koeppen's basic terms. This is also the general climate of the northern (or higher, or colder) half of Wolfe's Mixed Northern Hardwood Forest. For the beeches in East Asia, the most cold-tolerant populations of F. engleriana and F. crenata are found in localities with a Da/bf climate.

The situation of E North America should be addressed after the above complete discussion on the evolution in temperature adaptation of deciduous hardwoods and evergreen conifers in temperature adaptation. Wolfe (1979: 25-26) provided an excellent commentary on the forest vegetation of E North America. I shall begin my discussion with his major viewpoints in this respect, as follows:

First, Wolfe considered that the E North America is "anomalous" "in the almost exclusively broad-leaved deciduous (in some instances pines are dominants) forests of eastern United States". The extensive lowland (except the higher elevations of the Appalachians) region south of ca. 40 degrees N enjoys a Caf climate. In East Asia, the extensive Caf (lowland) region is covered by Notophyllous Evergreen Broad-leaved Forest. The relative position between, and the absolute latitudinal width, of the Caf, Daf, and Dbf regions are comparable between East Asia and E North America. However, the E North American Caf, Daf and Dbf regions differ from their East Asian correspondants in both major forest types and the distribution pattern of these forests. In E North America, there seems to be only one prevailing forest type. It is basically a mixed deciduous broad-leaved forest. Non-microphyllous evergreen hardwoods are almost absent. The few coniferous species

belong to Pinus and Tsuga. The characteristic canopy species of this forest type are oaks, beech(es), maples, birches, and hemlocks. Such a forest is observable in mesic habitats from Nova Scotia to C Georgia and C Alabama. The various variants of this forest type have different deciduous codominants. Sometimes some of these codominant species become so abundant that special forest types are locally recognizable. This forest type trends basically N-S. The three W-E trending temperature regimes decide the presence or absence, or the abundance of constituent species, to some extent. The more xeromorphic deciduous hardwoods, such as those of Quercus and Carya, are better represented in the western longitudinal belt. Hence, this belt is attributed to the deciduous hardwood forest region, and its northern and moister plateau portion is traditionally called "Mixed Mesophytic Forest". On the other hand, the more moisture-loving conifers are more abundant in the eastern longitudinal belt. Therefore, this belt is sometimes called the mixed deciduous hardwood and evergreen conifer forest. In East Asia, similar forests are normally seen as a narrow transitional belt between deciduous broad-leaved forest and evergreen coniferous forest. They bear no particular names in East Asia. Wolfe explained the predominant role of deciduous hardwoods in E North America by a meteorological factor: "Eastern North America, ..., is subjected to continuing, intense cold waves from the Arctic". He then emphasized the rather frequent occurrence of the very cold winter-temperature extremes in this general region to reach a conclusion: "It is probably this factor of prolonged cold spells in eastern United States that accounts for the existence there of broad-leaved deciduous forests rather than broad-leaved

evergreen forests.". It is clear that the same climatic phenomenon also explains the N-S trend of the only prevalent forest type, as described above, in E North America.

Second, Wolfe's ideas about the origin of the current forest vegetation in E North America are very instructive. In his words, "The development of many of the broad-leaved deciduous forests in southeastern North America probably involves the gradual elimination of broad-leaved evergreens during the late Cenozoic, leaving the broad-leaved deciduous element, formerly subordinate, as dominant." He further argued that: "By analogy, the secondary forest in the Notophyllous Broad-leaved Evergreen forest of Asia is composed primarily of broad-leaved deciduous trees along with pines. In this sense, the climax forests of much of eastern North America are, ..., secondary in nature." However, I have a different interpretation of the origin of the current forest vegetation of E North America. Wolfe implied the gradually intensified cold waves from the Arctic to have been very influential in the gradual disappearance of the original Notophyllous Evergreen Broad-leaved Forest in E North America. Nevertheless, I consider the globewide trend of cooling since the Upper Miocene to be the original and primary factor in repelling non-microphyllous, non-pioneer evergreen large hardwood trees from E North America. The increasingly intensified global glacial cycles and the "local" cold-waves in winter from the Arctic, since the Upper Pliocene, would have eliminated these evergreen hardwoods very rapidly during the cold phase of an early glacial cycle. They did not return to E North America during the successive interglacial simply because they had already gone

extinct in the region. The dry region around Texas and NE Mexico had long been a great barrier for the migration of mesic evergreen forest-trees since the Upper Miocene. Before reaching this turning point, the prevailing forest type in E North America would be the Mixed Mesophytic Forest. Mixed mesophytic forests similar to the current East Asian MMF are the most common warm-phase forest vegetation reconstructed from the Pliocene fossil assemblages in W Europe, the Caucasia, and C Japan. Geographic and climatic barriers in migration had caused the complete extinction of the major tree-species of the original mesic evergreen hardwood forests of E North America and Europe; they had also resulted in the substantial extinction (in E North America) and complete extinction (in most of Europe) of the major tree-species of the successive mixed mesophytic forests. In E North America, the remaining deciduous hardwood species of the original mixed mesophytic forest still form forests in the S Allegheny Plateau, S Appalachian Mts., and Ozark Plateau, etc. These forests are the nomenclaturally "typical" MMF in vegetation science. They are chiefly located west of the major divide of the Appalachian Mts., and are thus geographically within the western longitudinal belt of the "Eastern North American Forest Type". East of the Appalachian Mts., the supposedly stronger influence of the winter low extremes suppresses the growth of more thermophilic or more "relic" deciduous hardwoods of the North American MMF.

Third, it is clear that the major tree species of the "Eastern North American Forest Type" are from the Pliocene mixed mesophytic forest of E North America, and the climax forests formed by them are not "secondary" in nature. In East Asia, the first phase of secondary

forests in the Notophyllous Evergreen Broad-leaved Forest is chiefly represented by alders and/or birches in more mesic sites, or deciduous oaks and/or pines in more xeric sites. Pure or nearly pure stands are common. However, they are very seldom considered to represent region-wide climax forest types. Most of these pioneer species are supposed to have been wandering around within a very broad area for many millions, if not tens of millions of years. The deciduous habit of these hardwoods is most probably somewhere between dry-deciduous and cold-deciduous in ecological adaptation. In terms of ecological attributes, these East Asian species are highly shade-intolerant, very fast-growing, and very short-lived, whereas the major species of the forest in E North America are highly shade-tolerant, very slow-growing, and very long-lived. However, these two groups of species are similar in their high temperature-indifference and (hence) wide-distribution. It should be noted that the three first-mentioned ecological attributes of the major E North American species also characterize the major forest-inhabited congenetics in East Asia, so far as I know. As to the temperature-indifference of these two groups under question, I suppose that this trait had evolved independently under different conditions. For the current major E North American tree-species, the surviving populations during the cold-phase of each glacial cycle are supposedly the most cold-tolerant ones at that time. Therefore, their northernmost populations should have well coped with the new climatic condition during each interglacial. Through frequent reciprocal "training" of this sort during the Pleistocene, their current northern populations should show rather little differentiation in temperature-adaptation.

Their current southern populations will give the entire species even a broader range in temperature-indifference; this phenomenon is inherently associated with the generally rather low level of taxonomic differentiation of the southern populations of these species.

Fourth, for the current major E North American species, more precise starting-point climates immediately before the "first" significant climatic deterioration around the Pliocene/Pleistocene are not self-evident. It seems clear that the current N-S-trending distribution pattern of these species had taken shape no later than the Pliocene/Pleistocene, controlling by the similarly oriented winter-chills and the Appalachians. The current southern limit of these species is most probably determined by the current southern front of the winter-chills. Thus, the characterization of such southern ranges as under a Caf climate looks almost meaningless. Theoretically, at least two reasons preclude an attempt to trace back the historic bioclimates of these species interglacial by interglacial. The first one is: during each interglacial, the populations of each of these species were offspring of the most cold-tolerant populations surviving from the preceeding glacial. The second is: the different historic populations living in each interglacial (and glacial) would have had different ranges of temperature-adaptation. At this moment, I can only say that immediately prior to the first significant climatic deterioration, the ancient populations of these species would have lived under a C/Daf, but close to a Daf, climate. Such a deduction and estimate is applicable to the ancient populations of the two living subspecies of the American beech.

Fifth (and finally), the ecological evolution in cold-tolerance of the northern subspecies of the American beech cannot be compared with that of the East Asian beeches. The current geographic range of the genus Fagus in China is well south of the greatest limit of the continental glaciation of the Pleistocene. Hence, for the East Asian beeches, the evolution of temperature-adaptation is supposed to have progressed under "normally intense" competitive conditions. The subspecies grandifolia of the American beech clearly reaches the ceiling of the cold-tolerance (Da/bf) for a non-boreal deciduous hardwood tree-species. In this respect, its performance is even slightly better than F. crenata and F. engleriana in East Asia. Along with a few other trees, this beech seems to have adjusted itself readily to be closely concordant with the new environment in each interglacial. Lax competitive environments of the two northern subspecies of the American beech in the Pleistocene makes a comparison of the ecological evolution in temperature-adaptation between them and the East Asian beeches not very meaningful.

Now finally comes the proper time to discuss the ecological evolution of F. sylvatica. The first thing I can say is that the situation of the typical European beech is essentially similar to that of the American Gray beech. The second thing is that the overall ecological evolution of F. sylvatica should be discussed within the proper context of the evolution of the forest vegetation in Europe since the Upper Miocene.

The prevailing forest type in most of Europe in the Middle

Miocene is the Notophyllous Evergreen Broad-leaved Forest, according to the information derived from numerous fossil assemblages. The Upper Miocene witnessed a transition between the former forest type and the MMF in most of Europe. During the Pliocene, the MMF normally occurred under a presumed Caf climate; whereas a deciduous broad-leaved forest (DBF) was present under a presumed Cbf climate (see Mai & Walther, 1988: 221). It seems clear that the major oscillation in temperature during the European Pliocene, which governed the change in vegetation type, affected mainly the summer temperature. The alternation between the MMF and DBF types does not seem to have been substantially influenced by the sometimes occurred climatic fluctuations in summer rainfall. According to Palamarev (1989: 93), "The major part of the Paleomediterranean woody plants appears in Miocene mixed mesophyllous and mesoxerophyllous, evergreen and deciduous forests."

The European Pliocene MMF was rich in Taxodiaceae (see Suc & Zagwijn, 1983; Mai & Walther, 1988; among others). Although the taxodiaceous plants persisted into the mid-Upper Pliocene (to ca. 2.5 my BP) in W Europe, they were particularly abundant during the Lower Pliocene. Hemlock and beech were among the major elements of the European Pliocene forests. The former was particularly associated with the DBF, whereas the latter was better represented in the MMF. Hemlock persisted into the Pastonian Interglacial (ca. 1.35-1.15 my BP ?) in W Europe; it has never recurred in Europe since then, so far as I know. In the W and C European fossil assemblages of the Upper Miocene age, beech(es) were often the (co)dominant elements of the DBF. During the Upper Pliocene, the first significant glacial cycle (since the Upper

Miocene onward) began at ca. 2.5-2.4 my BP. The European MMF disappeared forever within this period. The successive major warm period: Tiglian Interglacial Complex, was present from ca. 2.05-1.95 to ca. 1.70-1.65 my BP. It is subdivisible into three phases. After the middle cold phase, beech did not return to W and C Europe until the late part of the "Cromerian Interglacial Complex" (ca. 0.80-0.35 my BP). Later, it occurred in the Holsteinian (= Hoxnian, and Gortian) Interglacial (ca. 0.250-0.195 my BP). During both periods, the pollen values of beech were low. Beech was not recorded in the W and C European forest in the last interglacial: Eemian (=Ipswichian; ca. 0.130-0.075 my BP). After the coldest period of the last glacial, the first significant expansion of beech populations in Europe occurred in SC Balkan Peninsula, around 9,000 yr BP. The continuous populations extended rapidly northwestward along the Dinaric Alps to reach the southern hilly region of the Alps. They then went into C Europe by way of the eastern flank of the Alps, at about 7,000-6,500 yr BP. Another significant spreading evidently initiated in Romania at around 7,000 yr BP. These populations met with the above-mentioned ones no later than 6,000 yr BP. The "Romanian populations" became the dominant forest vegetation in the Balkan Peninsula no later than 3,000 yr BP, and then showed a tendency to a northward extension or shift. Now the land-area covered by natural beech populations is ca. 40,000 square km in Yugoslavia, ca. 20,000 square km in Romania, ca. 17,000 square km in France, ca. 11,500 square km in Germany and Austria, ca. 6,200 square km in Bulgaria, etc.. [For the most critical references on the geological history of beech in the European Pleistocene, see Godwin, 1956: 205-209;

1975: 273-276; Huntley & Birks, 1983: 191-194; etc..]

To my poor knowledge, the macrofossil records of beech in the European Pleistocene are also poor. Beech cupules and leaves have been found in the later part of the "Cromerian Interglacial Complex" in England. Five fragmentary beech cupules have been found in an Irish Holsteinian sediment. It seems likely that beech was absent from W and C Europe during a period from ca. 1.90-1.80 my BP to ca. 0.50 my BP. of the Pleistocene. In the area surrounding W and C Europe, an Eemian pollen profile in Bulgaria yields 120 % beech pollen. [The typical European beech is "generally recognized as seriously under-represented by its pollen frequency in relation to other trees" (Godwin, 1956: 206). The American beech growing outside Mexico is among the species that "do not conform to the traditional definitions of over-, equal-, and under-representation" (Delcourt et al., 1984: 95).] During the period from the beginning of the last glacial to its coldest phase, that is, ca. 75-25 ky BP, beech pollen was not rarely found, such as in S Italy, Greece, etc..

Here comes a problem about the specific identity of these beech remains, both macro- and micro-fossils. The beech cupules found in the Irish Holsteinian are associated with pollen of Rhododendron and Abies. Firs and spruces are the most significant associates of the W Eurasian beeches nowadays. In the highland Balkan Peninsula, the Moesian beech constantly associates with Abies alba to form the typical forest type at middle elevations. At high elevations, the typical European beech and Picea abies subsp. abies are the two dominant species of the forest; either of them is able to form pure forest under its most favorable

conditions. Among the six fir species now growing in Europe, only Abies alba is widespread. This fir is chiefly found in C and E European highlands. It is almost true that wherever Abies alba is common, the beech also abounds. Two species of Picea are native to Europe today. Within the current geographic range of beech, there is only one wide-ranging spruce: Picea abies subsp. abies. It often shares dominance with the typical European beech in the highest forest belt in non-boreal Europe. In Europe, the Pleistocene fossil history of Abies alba and that of Picea abies subsp. abies are similar to that of beech, as discussed above. These three are further consimilar in the pattern of their initiation and early development. The Turkish beech covers about 8 % of the forested land in Turkey. The western populations of Abies nordmanniana subsp. nordmanniana show a very close geographic range, altitudinal range, and optimal habitat, to the Turkish beech, along a W-E belt (W of ca. 36 degrees W) in N Anatolia. In the humid region along the eastern coast of the Black Sea (E of ca. 38 degrees W), the vast majority of the populations of the Caucasian beech are centered, where they cover 125 % of the forested land. Picea orientalis and the eastern populations of Abies nordmanniana subsp. nordmanniana are confined to this region. [It is notable that in the general region from Anatolia to the Caucasus, the genera Picea and Abies are only represented by three species: Picea orientalis, Abies nordmanniana, and Abies cilicica. Abies cilicica is endemic to the more humid W-E belt in SC Anatolia, where some mixed beech populations are isolated.] It is also almost true that wherever either or both of these two conifers are common, the Caucasian beech abounds. No spruce or fir is associated with the

typical European beech in the lowland W and C Europe.

Another interesting plant should be mentioned in this connection. Rhododendron ponticum is the only species of Rhododendron section Ponticum growing outside North America. Its three major infraspecific entities are considered to differ only insignificantly (see Stevens, 1978: 93). The subspecies baeticum is endemic to the Iberian Peninsula. The variety brachycarpum is found only in Lebanon. The subspecies ponticum is latitudinally widespread from E Balkans, through N Anatolia, to W Caucasia. This large evergreen shrub (to 10 m tall) is almost confined to beech-dominant forest, in which it is often a codominant species of the secondary layer. Stevens (1978: 93) considered its absence from the A5 geographic grid of Turkey (ca. 34-36 degrees W) to be "genuine". His opinion in this respect is supported by a fact that the grids A5 and A6 connect the more humid eastern coast of the Black Sea and the relatively drier NW Anatolia. Many plant taxa show a depressed abundance in this region, regardless of whether a (concomitant) taxonomical differentiation is clear or not. In the case of F. sylvatica, morphologically typical individuals of subsp. hohenackerana are only found east of ca. 38 degrees W. Returning to my discussion on the ecological evolution of F. sylvatica, it seems clear that Rhododendron ponticum is highly relevant. The current distribution pattern of Rhododendron section Ponticum implies that R. ponticum is a so-called Tertiary relic. The current distribution pattern of R. ponticum in turn implies that a similar distribution pattern had most probably been present no later than the Pleistocene, if not earlier. Since Rhododendron ponticum is an element of mesic forest, its

association with other important members of mesic forests in the general region surrounding W and C Europe, such as beech, fir, and spruce, might have extended far into the geological past. Although the individualistic concept of the forest association should be always borne in mind, the surviving members of the European MMF and DBF can only be supposed to have remained together in a latitudinally oriented mesic forest during glacial cycles. Therefore, the co-occurrence of beech, fir, and rhododendron in a fossil assemblage from the later British "Cromerian Interglacial Complex" may not be incidental. Judging from the present geographic location of the several beech entities that conform to the above-mentioned concept, the Moesian beech appears to be the most proper candidate for the beech that had grown across at least the western part of the European continent during the earlier time of the Middle Pleistocene. This supposition also explains the great representation of the Moesian beech or its genetic influence in the isolated beech populations in the Amanos Mts. and Crimea.

An important clue to the flourishing of the typical European beech comes from itself. Compared with the Moesian beech, the typical European beech has leaves smaller, more crenate (or less serrate), thicker, and more blunt in apex and acme. These traits could be considered collectively as a manifestation of drought-adaptation. Under the prevailing climate of the current optimal habitat of the typical European beech in W and C Europe, such a syndrome of drought-adaptation looks weird. On the other hand, these traits could be well perceived to have evolved under a temperature regime not very different from that currently prevails in S Europe, and a precipitation regime with more

summer rain. The climate of the mediterranean region became more and more similar to the present one after the Upper Pliocene, through the somewhat regularly intensified Milankovitch Forcing. The drier and drier summer during the consecutive interstadials of glacial periods would have not been favored by the populations of the Moesian beech at that time. Some western populations of the Moesian beech would have borne leaves more and more similar to those typical for the present-day typical European beech. However, these newly evolved, more drought-tolerant marginal populations could not substantially expand their range during the successive interglacials, because the summer humidity at that time was still adequate for the morphologically unchanged populations of the Moesian beech. The Eemian Interglacial was warmer and drier than the current one (Flandrian). It is also most probably the warmest interglacial since the Middle Pleistocene. The drought of such a climate might have been responsible for the lack of the Moesian beech even in the Balkans; and the "ancestral" populations of the typical European beech were perhaps checked by the warmth of this climate. The abundant beech pollen in a Bulgarian Eemian sediment, as mentioned previously, is very likely to have been shed by the Turkish beech.

The expansion of beech in Europe during the present interglacial needs some discussion. Although the overall trend of climatic change during late-glacial and early postglacial is toward a warmer and more humid climate, various combinations of different temperature and precipitation regimes had occurred. In the case of beech, the two major original populations were at similar latitudes, and were not very far away from each other. Nevertheless, they were "activated" at different

time-points by different climates, and then showed different expansion patterns. This fact clearly implies that these two original beech populations had different ecological traits. A detailed comparison of the two "activating" climates and the two current climates associated with these two original populations is beyond the scope of this monograph. In all probability, the SC Balkan population belongs to the typical European beech, and the "Romanian population" belongs to the Moesian beech.

Now it seems clear that the present-day forest vegetation in most of Europe has a Pleistocene history far more complex than that in E North America. In non-boreal E North America, there are one spruce, one fir, and two hemlocks. Tsuga canadensis has evidently significantly modified its ecological traits to "accommodate" the prevailing climatic change during the Pleistocene. It thus now assumes an extensive N-S geographic range, and well appears as one of the most important tree species in the "E North American Forest Type". Tsuga caroliniana and Abies fraserii are both confined to the highest elevations of the Appalachians. They can be well presumed to have roughly maintained their pre-Pleistocene ecological adaptation. The geographic range of Picea rubens is similar to that of the American Gray beech, but its range of temperature adaptation is in the cold end of the range of the American Gray beech. With reference to its relative ecology to beech in the same region, this spruce is "normal". As a conclusion, the overall ecological situation of the non-pine pinaceous conifers in non-boreal E North America is different from that in non-boreal Europe. However, it should be noted that Europe has preserved five "relic" species of Abies.

Now I will turn to the non-pine pinaceous members in East Asia. Three genera are endemic there: Cathaya, Keteleeria, and Pseudolarix. Many hemlocks are present. When non-pine conifers abundantly occur in the upper portion of a beech forest, or occur as a coniferous forest above a beech forest, the vast majority of these conifers belong to a hemlock. The optimal habitats of various spruces are generally elevationally higher or more northern than those of hemlocks. At least within the geographic range of the genus Fagus, the optimal habitats of various firs are still elevationally higher or more northern than those of spruces. I do not expect to see any beech species well intermingles with any fir species in East Asia, as can be sometimes seen in E North America, or normally seen in W Eurasia. It can be argued that some of the important forest-trees in non-boreal E North America, and most of the important forest-trees in non-boreal Europe have considerably modified their ecological traits during the Pleistocene to assume their current significant ecological niches. It follows that comparisons on ecological adaptation and ecological niche among the congeneric species respectively growing in the non-boreal area of these three geographic regions are not pertinent to the context of their taxonomical differentiation at higher levels. Simultaneously, the overall evolution of this kind of species should be discussed within the context of the climatic, geological, and geographic changes of the respective geographic region occurring after the species under enquiry first appeared there.

The above conclusion is certainly applicable to beech. In Europe, F. sylvatica is not found in boreal area or mediterranean area.

It is clear that most, if not all, of the important forest-trees growing in this region have experienced the reciprocal climatic "training" during the Pleistocene. What I stress here is that the "training" provided by the Pleistocene to most of Europe clearly differs from it had offered for E North America, because of the geographic position of the former. The southern margin of Europe is latitudinally about 10 degrees higher than that of E North America. Moreover, at least the western third of Europe is close to the western margin of a continent, whereas the region of E North America under enquiry is close to the eastern coast of a continent. Chiefly due to the influence of the North Atlantic Current, the climate of the western third of Europe has only one counterpart in the Northern Hemisphere: that present in the similar latitudinal belt of NW North America. This Cb climate is oriented along the direction of the associated ocean current, whose strength determines the northern limit of this climatic region. In essence, this climate is governed by a northward climatic forcing. In E North America, another kind of southward climatic forcing dominates the distribution of major forest-trees, but it does not appreciably modify the distribution patterns of the major climatic regions, particularly in terms of temperature regime. However, the impact of the climatic forcing on Europe is so powerful that it offers only one temperature regime for the region under its influence.

Another climatic forcing dominates the climate of the region surrounding the Mediterranean Sea. It shifts the seasonal distribution of rainfall to such an extent that the most significant plants that can grow there are very xeromorphic small trees or thorn-shrubs. According

to Palamarev (1989: 105), "Only during the Late Miocene and Pliocene, a semi-arid climatic zone was formed between 37 degrees and 45 degrees N latitude with more prominent sclerophyllous woody coenoses.". He further commented that "In the Late Pliocene the differences between the W. and E. Mediterranean floristic areas are already apparent, differences which further increase during the Pleistocene.". In fact, the higher summer temperature in the eastern Mediterranean region also characterizes the northern inland non-Mediterranean area.

The current non-boreal inland Europe has a relatively "normal" climate. Being less influenced by these two climatic forcings, the climate is more concordant with the general climatic principles, which are chiefly based on geographic position, latitude, and topography. It is chiefly different from the above-mentioned areas in W and S Europe in its colder winter (Daf, Dbf, and Bsk). It is notable that there is a latitudinally extended steppe area (Bsk) north of the Caucasus Mts.

For the currently non-boreal and non-Mediterranean Europe, Mai & Walther (1988: 216-219) and Mai (1989: 86) recognized two Pliocene floristic regions: Western European and Southeastern European-Pontic. [The relative positions refer to purely natural geographic locations.] They are basically latitudinally juxtaposed, with the Balkan Peninsula being the transitional region. This division is particularly interesting because it was originally based on the distribution of aquatic and swamp herbaceous plants, then found to be compatible with the paleofloristic division of woody plants. The inherent reason for this similarity seems to reside in the primary significance of the moisture regime in the development of plants during the European

Pliocene.

According to the current knowledge on fossil vegetation and the reconstruction of paleoclimate, it seems clear that all of the relevant major climatic changes might have exerted an appreciable influence on European plants no later than the Upper Miocene (an Epoch from ca. 12-11 to ca. 5.4-5.2 my BP). A globewide cooling trend is clearly observed since the uppermost Miocene. Small-scale climatic fluctuations had extended into earliest Upper Pliocene (= Piacenzian, or Romanian, or Egrissian + Gurian; an Epoch from ca. 3.4-3.3 to ca. 1.67-1.65 my BP). During a period from ca. 8 to ca. 3.2-3.1 my BP, the forest vegetation in non-borealand non-Mediterranean Europe seems not to have undergone drastical changes. However, it may be true that during this period, MMF would be more prevalent in the relatively warmer and damper western part, whereas DBF would be more common in the colder and drier eastern part.

It seems proper to mention the situation of Caucasia in this connection. Since the Upper Miocene, tectonic activities elevated and connected the "Caucasian Archipelago" in the Paratethys Sea to form the primeval Caucasus Mountains. Prior to this time, the forest vegetation in this general region was a rather wet Notophyllous Evergreen Broad-leaved Forest, in which many thermophilous conifers and deciduous hardwoods were common. Beech was found in this forest, but only in a trivial to negligible amount. [Some islands at this time might have been about 1,000 m high.] Due to the very rapidly elevated W-E mountain chain, the general climate in the Transcaucasus seems to have changed only rather slowly thereafter, chiefly in the moderate lowering of

temperature. Since then, the Transcaucasus, particularly its western part, began to assume its "refuge" appearance, in terms of both flora and vegetation. During the uppermost Miocene and Lower Pliocene, the luxuriant MMF in at least W Transcaucasus still contained beech as an insignificant element. The first really drastic change in the plant life in W Transcaucasus seems to have occurred during the earlier half of the Upper Pliocene (the Egrissian stage of the Black Sea stratigraphy, most probably equivalent to the Reuverian stage of the North Sea stratigraphy). The more intense and more frequent climatic cycles that had characterized this period made species of Tsuga, Picea, and Abies become dominant in the cold-phase forest. The importance of beech also increased considerably. Just before the beginning of the Pleistocene (during the latest Gurian stage of the Black Sea stratigraphy), the climate in W Transcaucasus supported a beech-hemlock-fir-spruce forest at middle elevations. This forest association is supposed to have assumed the fundamental composition and structure of the prevailing forest currently seen in the same localities. However, the forest at low elevations still experienced drastical changes during the Pleistocene. It finally lost all MMF-associated conifers after the initiation of the last glacial (Oxygen-18 stages 4 to 2; = Weichselian, Wurm, Dalian, Wisconsinian), along with some other deciduous (and evergreen) broad-leaved trees. At about the same time, hemlock disappeared from Caucasia, marking the extinction of the genus Tsuga in Europe. [For the critical references of the preceeding discussion, see Tumajanov, 1971; Shatilova & Ramishvili, 1984; Stuchlik & Shatilova, 1987; among others.]

The above discussion on the vegetational history in the Caucasia clearly points to a northern origin of beech in the Upper Miocene "refuge" there. With regard to the phylogeny of the beech that dominated the pre-Pleistocene mid-elevational forest of the Caucasia, which is almost certainly the immediate ancestor of the current populations of the Caucasian beech, however, there exist two possibilities. The first one is that it is a derivative of the Miocene beech found in primeval Caucasia. The second possibility should be discussed within the context of the geological evolution of Anatolia. Prior to the Miocene, both the Black Sea and Caspian Sea were roughly speaking part of the Paratethys Sea, and the only lands in the general area of the current Anatolia were scattered low-lying islands. During the Miocene, the stratum of the current W Anatolia was elevated as a continuous land. However, the paleo-islands located in the current E Anatolia were elevated and thus connected with the Caucasia and W Anatolia, during the earlier time of the Pliocene. To the west, the northern portion of the current Aegean Sea was connected with both of the Balkans and Anatolia during the Pliocene, by extensive land. As a result, the humid N Anatolia (N of and/or within the Pontic Range) could have been used by plants to migrate between the Caucasia and the Balkans, during the warm phases from the Pliocene onward. Davis (1971) proposed a term "Anatolian Diagonal" to refer to a remarkable floristic break of the flora of Turkey at specific and generic levels. This demarcation line is supposed to have resulted from the the geological history of Anatolia. However, the associated plants are mostly herbaceous and are supposed to have migrated from the Irano-Turanian

floristic region. The Turkish beech is now absent from Caucasia (incl. Lazistan). Wherever the Turkish beech is found, I see no Caucasian beech. This observation may support the hypothesis that the immediate ancestor of F. sylvatica subsp. hohenackerana migrated into the primeval Caucasia from the north no later than the boundary between the Middle and Upper Miocene, and developed as a dominant forest-associate there by the end of the Pliocene.

Now I shall comment on the ecological evolution of the Turkish beech. All of the differences between the leaves of the Caucasian beech and those of the Turkish beech indicate a xeromorphic evolution that had caused the associated changes from the former to the latter. Indeed, the climate under which the Turkish beech flourishes is generally drier than those foster any other W Eurasian beech enumerated previously. It assumes a scrub-like stature and/or grows in thickets in rather dry habitats (in W Anatolia) where presumably no other W Eurasian beech can thrive.

The remarkably spathulate-foliaceous cupule-appendages of subsp. orientalis (= the Turkish beech) are clearly derived from those prevalent on the cupule-valves of another two subspecies. However, the characteristic leaves of subsp. orientalis can only be perceived as having been modified under a drier environment from those diagnostic of subsp. hohenackerana. In this connection, it should be noted that subsp. orientalis and subsp. hohenackerana nowadays occupy different geographic ranges. The typical Caucasian beech only grows in the Caucasia (incl. Lazistan), whereas beech individuals with both leaves and cupule-appendages typical for the Turkish beech are only found in

Anatolia and some isolated localities in the southeasternmost Balkans, based on the beech collections at my disposal. Another fact is that no typical Turkish beech is found growing east of Davis' Anatolian Diagonal. The lack of map-sympatry in this case perhaps can be explained by the significant difference between these two subspecies in moisture adaptation. The difference in moisture regime currently present between W Cacausia and the N Anatolia west of Davis' Anatolian Diagonal can be supposed to have been existent in some period of the Pleistocene, or even the Upper Pliocene. It thus follows that the immediate ancestor of the Turkish beech might have lived somewhere close to the western coast, rather than the always moist eastern coast, of the Black Sea. At least the western part of the current drought belt north of the Caspian Sea and Black Sea can reasonably be supposed to have experienced a less drier climate sometime in the Pliocene. If so, some beech populations genetically similar to the Pliocene ancestor of the Caucasian beech would have had a chance to migrate around this general region. Some of them would then probably have left derivatives morphologically and ecologically similar to the current Turkish beech somewhere in this general region. Those distributed close to the western coast of the Black Sea would have had much better chance to survive under the subsequent unfavorable climatic phase, because they could migrate along the western and southern coasts of the Black Sea. The overall Pleistocene climate along at least the southern coast of the Black Sea can be reasonably supposed to have never been very unfavorable for these populations. The competitive situation there can also be reasonably supposed to have been rather lax during the Pleistocene,

because of the limited number of species surviving previous vicissitudes. If such populations however had moved into W Caucasia, the more competition-oriented ecological environment would have had enough chance to eliminate these more tolerance-oriented plants subsequently. Today, the northward expansion of the Turkish beech along the western coast of the Black Sea is checked by the very dry Valachian Plain where steppe prevails. West and northwest of the current Balkan stations of subsp. orientalis, the general climate is clearly more suitable for subsp. sylvatica. Finally, I shall suppose a time of origin for F. sylvatica subsp. orientalis, based on my foregoing discussion. That is: no earlier than the Lower Pliocene; most probably during the Upper Pliocene; a Lower or Middle Pleistocene time is also possible.

To close the discussion on the current geographic range and ecological adaptation of F. sylvatica, some final statements regarding the overall evolutionary situation of the major members of the non-boreal and non-Mediterranean forests in most of Europe (W of Caucasia) may be pertinent.

First, these tree-species are derivatives of the most cold-tolerant populations of the surviving members of the deciduous broad-leaved forest that had flourished before the severe glacial cycles came into being.

Second, because of the mainly W-E trending mountain-chains in S Europe, and the drier and drier growing-season climate in the Mediterranean region, those surviving populations could have persisted only within a very narrow W-E belt between these two hostile climatic

regions during interglacials. The sheltered habitats in the S European mountains would have been the best localities available for them.

Third, the cold-phases within a glacial cycle would be the time during which some evolution, mostly at infraspecific levels, would have begun in these survived populations. The marginal populations with new traits would have had a chance to develop further their own genetic characterization during the coming warm phase of the same glacial cycle. Thus, the genetically more distinct marginal populations of these recently expanded derived populations would have had a chance to become isolated as new entities during the coming cold phase of the same glacial cycle. Because the Pleistocene is dominated by the so-called "glacials", the accumulated geological time of this sort of climatic cycle (within a glacial cycle) may be long enough for at least the subspeciation of tree-species.

Fourth, the evolution of many of the surviving populations of those DBF-associated trees would have been significantly influenced by the more and more distinct Mediterranean climate to the south. The evolution of the typical European beech may be well of this category. The number of new entities that are derived from these surviving populations and can be characterized as typical Mediterranean elements would be very few, if any. Some surviving populations of some originally relatively more mesic trees would have persisted in some well sheltered enclaves during the entire glacial cycle, with their gross morphology and ecological amplitude little changed. The Moesian beech belongs to this category.

Fifth, during the short time-span of the so-called

"interglacials", evolution of the plants that "re-colonized" the non-boreal Europe may not be significant. The lax competitive environment would have also slowed down the evolutionary rate.

Sixth, the distribution pattern of some of the major forest-trees at the climatic optimum of interglacials might not precisely reflect the optimal climatic regime for these trees. The plants persisting in refuges in the Iberian Peninsula would certainly have a better chance to settle in non-boreal W Europe, because they had lived under the influence of the North Atlantic Current for a period of time. However, if the availability of proper trees is limited, some trees expanding their range from eastern refuges would have a chance to extend westward into W Europe, inasmuch as some of the climatic traits there do not differ significantly from those characterizing their optimal habitats in more inland Europe, whereas the climatic conditions new to them do not limit their growth. I think that the typical European beech is among these few important trees. This supposition can also at least partly explain the lack of non-pine coniferous forest in W Europe where a Cbf climate prevails.

Seventh, it seems rather clear that anthropogenetic disturbance had greatly helped the typical European beech reach its current dominance in W (and NW) European lowlands. Beech populations had already well settled around the transitional area between the C European highlands and the W and NW European lowlands no later than ca. 5 ky BP, after a rather rapid expansion with a rather stable rate. The rate of expansion of beech populations then slowed down for a while, without significant occupation of new habitats. The overall geographic and

density patterns of the subsequent expansion of beech populations roughly correspond to those of the colonization of human populations in Europe. Godwin (1956: 208-209; 1975: 276), Huntley & Birks (1983: 193-194), Bottema (1988: 200-203), among others, have clearly and convincingly expressed their conviction that "The failure of beech to expand directly into lowland northern and western Europe is unlikely to have been climatically controlled." (Huntley & Birks, 1983), and that the agricultural activities had played a primary role in "triggering" the expansion of beech after about 5 ky BP in W Europe. Godwin (1956; 1975) stressed that the artificial removal of mixed oak forest would have left land suitable for beech. Huntley & Birks (1983) mentioned the "coincidence of the expansion of beech into the European lowlands after 5000 BP with the elm-decline". Bottema (1988) first suggested the "weedy" nature of the typical European beech in W and NW European lowland forest. E. Weeda (cited in Bottema, pers. comm., 1991 Feb 4) suggested that the typical European beech filled the niche previously occupied by Tilia in the lowland forest, after linden forest was destroyed by man.

Eighth, the "weedy" status of the typical European beech in lowland W and NW Europe is strengthened by the nutrient-poor soils frequently present in considerable area there. The available information shows that this beech can thrive on dry, poor, and shallow soils, provided that the relative humidity is high enough. It seems to be capable of growing on any well-drained (non-sandy) substratum. All these observations mentioned in the items 6, 7, and 8 collectively depict a plant that would be normally called a weedy species.

Ninth (and finally), such weedy trees are perhaps very few in the forested, non-boreal, and non-subtropical Northern Hemisphere. Among the members of this category, the typical European beech is probably the most outstanding and interesting one. This beech dominates the highest forest belt in many Balkan mountains. It also frequently occurs there as the only timber-line species. These demonstrate the extraordinary ecological characterization of the typical European beech in its tolerance to another commonly seen combination of harsh site conditions. However, the "super weediness" of this plant perhaps would not be readily appreciated without an adequate background.

TAXONOMIC REMARKS:

The taxonomic history of the beech populations growing in W Eurasia is basically a history recording the great effort of many taxonomists in their attempt to characterize, and clarify the distribution of the beech with prominent foliaceous cupule-appendages. In 1864, A. de Candolle validly published the nomen nudum proposed by Hohenacker in 1838: F. sylvatica var. macrophylla. As implied by the epithet, de Candolle assigned the Caucasian beech collections with large leaves (to 15 cm long) and numerous lateral veins (9-14) to this variety. None of the Caucasian collections under his study is fruiting. De Candolle was the first who remarked the spatulate-foliaceous appendages on the cupule-valves of beech collections from Anatolia, N Iran, and Japan. He described a variety: F. sylvatica var. asiatica, to accommodate these collections, without mentioning their leaves. However, de Candolle wrote: "An ad var. Asiaticam referendae ?", to

conclude his taxonomy of the variety macrophylla. The essence of de Candolle's taxonomy, if not the nomenclature, was followed by most subsequent authors. Many authors thus even conjectured the presence of this kind of beech populations somewhere between W Eurasia and Japan.

Lipsky proposed a name F. orientalis for beech populations growing in Anatolia, Caucasus, and N Iran, in 1898. He emphasized the differences between his new species and F. sylvatica (= the common European beech growing in W and NW Europe) in features of the perianth-tube of male flower and features of cupule-appendages. He did not describe the leaves of F. orientalis. The only comment on the leaves of F. orientalis is expressed in a comparison: "Quoad folia fere nullum discrimen video inter F. silvaticam L. et F. Orientalem m., nisi in hac folia adulta magis coriacea.". He correctly excluded the common Japanese beech (= F. crenata subsp. crenata) from his taxonomic concept on beech populations growing in W Eurasia. On the other hand, his concept in keeping all beech populations growing east of the Balkan Peninsula in an entity in contrast to the other entity incorporating beech populations growing west of the Balkan Peninsula has caused a century-long confusion.

H. Winkler (1901: 4-5) roughly agreed with Lipsky's concept of beech populations growing in W Eurasia, with a more detailed study on leaves, including the morphology of epidermal cells. Based on the principle of priority, Winkler elevated de Candolle's name F. sylvatica var. asiatica as F. asiatica, to replace Lipsky's F. orientalis.

Palibin (1908: 378) was the first one who well appreciated the differences between the Turkish beech and the Caucasian beech in both

leaves and cupule-appendages. He admitted the presence of two beeches in Caucasia: F. asiatica and F. hohenackerana, and he thus reassigned the plants assigned under the name F. orientalis by Lipsky (= those assigned by Winkler under the name F. asiatica) into these two entities. For the W Eurasian beech populations growing east of the Balkan Peninsula, Palibin progressed along the road paved by de Candolle in the fact that he listed F. sylvatica var. macrophylla (Hohen.) A.DC. as a synonym of his new name F. hohenackerana. His description is pertinent: "Fagus foliis magnis, rhomboideo-ovatis, basi cuneatis, margine undulato-dentatis, apice elongato-acuminatis, nervis secundariis (utrinque 9-14) rectis vel vix curvatis, divergentibus; cupulis ebracteatis; nuculis conicis. - Hab. Caucase oriental, Transcaucasie et Perse.". Palibin clearly remarked the obvious difference between the Turkish beech and the Caucasian beech in cupules. However, very few subsequent authors have paid due attention to Palibin's work, except W. H. Camp, Czechott, and Browicz. It should be borne in mind that Palibin and Camp are the only two who had made great efforts toward a monograph of the genus Fagus.

Probably there are four reasons that could explain the failure of Palibin's contemporary Russian colleagues to distinguish the Caucasian beech from the Turkish beech. First, their attention was primarily on the taxonomy and geography associated with the so-called common European beech and the beech populations growing east of the Balkan Peninsula. Second, the lower appendages on the cupule-valves of the Caucasian beech may appear as linear-foliaceous in the eyes of some taxonomists, although they are actually just very-long lanceolate, and never assume a

spathulate form. Thus, these appendages can be perceived as close to or not significantly different from those spathulate-foliaceous appendages of the prevailing beech populations growing in Anatolia. Third, the geographic range of the Caucasian beech would have encouraged Russian taxonomists to regard these populations as representing the outliers of the Turkish beech. Fourth, the abundant occurrence of a variety of the Caucasian beech, Czechtz's beech, in Caucasus and W Anatolia would have most probably confused any taxonomist who tried to differentiate the Caucasian beech from the Turkish beech in the past.

During the 20s and 30s of this century, the study of the W Eurasian beech populations was focused on the taxonomy of the beech populations in the Balkan Peninsula, Crimean Peninsula, and Caucasus to a lesser extent, on the basis of recognizing two species (F. sylvatica and F. orientalis) in W Eurasia. Among the relevant publications, the following are important: Czechtz (1932; 1933; 1935), Domin (1932), Grossgeim (1930), Hjelmqvist (1940), Poplavakaja (1925a; 1925b; 1928), Stefanov (1927), Stojanov (1929), Stojanov & Stefanov (1923), Turrill (1930), Wulff (= Vul'f, 1925; 1932; 1936), Wulff & Zyrina (1924; 1925).

After this period of extensive and intensive study, the nearly consensus viewpoint on the taxonomy of the problematic beech populations in W Eurasia was to assign the large-leaved populations in the Balkans to the entity "moesiaca", and the Crimean beech populations to F. x taurica (= F. sylvatica x F. orientalis). The epithet moesiaca may be used as a specific name, or referred to as a subspecies or a variety of F. sylvatica.

The proposal of a new combination F. sylvatica subsp. orientalis,

validly published by Greuter & Burdet in 1981, marks a new era of the taxonomy of the W Eurasian beech populations. Alden (1986: 52) has gone so far as to say that "Subspecies sylvatica and ssp. orientalis are in fact typical geographical races, having a broad range of intermediates in the zone of contact."

I agree that to consider the Turkish populations with prominent spathulate-foliaceous cupule-appendages to be part of the single beech species in W Eurasia is conceptually useful. On the other hand, the taxonomic and evolutionary situation of the Turkish beech within such a comprehensive species should be considered within the context of the complex evolutionary history of the three subspecies (as recognized here) of F. sylvatica in W Eurasia.

It is necessary to ordinate the living beech populations in W Eurasia before I can organize them into subspecies. So far I can distinguish five major population-groups in this region: the typical European beech, the Moesian beech, Czechtz's beech, the Turkish beech, and the Caucasian beech s.s., from west to east. Only spathulate-foliaceous cupule-appendages can clearly differentiate the Turkish beech from the remaining four. Thus, it is not surprising that they serve as the only reliable trait for many authors to distinguish the so-called common European beech from the so-called oriental beech. My perception of the existence of five population-groups is chiefly based on the differences in leaves. A good key to these five groups based on leaves is hardly possible. Nevertheless, a characterization of the more diagnostic leaves and the geography of them is given as follows:

CAUCASIAN BEECH S.S.: large-(medium), (8)-10-15-(17) cm long;

thin; nearly obtrullate to nearly rhombic; apex acuminate; acme acuminate; base narrowly cuneate; basal margin straight or even slightly concave, tapering straightforward into the very-base or abruptly incurved as a small, clearly cordate very-base; secondaries 10-15-(17); margin varying from serrate to slightly serrate to slightly sinuous; long, silky hairs densely persistent on the major veins of the lower surface. [With numerous very-long linear, acute-apexed, foliaceous, drying purplish/brownish, inconspicuously veined appendages on the lower half of the cupule-valves.] In entire Caucasia and N Iran. Within Caucasia, particularly abundant in W Transcaucasus.

CZECZOTT'S BEECH: large-medium, 8-12-(15) cm long; thin-thick; roughly obovate, sometimes close to nearly rhombic or elliptic; apex acuminate-acute; acme acute-(obtuse); base together with the very-base assuming a characteristic contour, with the margin lower than the broadest portion slightly convex to straight then slowly incurved as a rounded very-base; secondaries 10-15; margin varying from slightly serrate to slightly sinuous to slightly crenate; long, silky hairs at least observably persistent on the major veins of the lower surface. [Cupule traits undistinguishable from those of the Caucasian beech.] In southeasternmost Balkan Peninsula (particularly abundant in Turkey-in-Europe), W Anatolia (abundant), Amanos Mts., Crimea, and N Caucasia (abundant).

MOESIAN BEECH: medium-(large), 10-14 cm long; thin; broadly elliptic/oblong to broadly rhombic; apex acute-(acuminate); acme acuminate-(acute); base (together with the very-base) rounded to cuneate; secondaries 8-12-(14); margin varying from slightly serrate to

slightly sinuous. [Very-long linear, foliaceous, drying purplish/brownish, inconspicuously veined appendages narrower, seldom present on above the basal portion of cupule-valves.] In SE Europe (abundant, at lower elevations of the montane region), Amanos Mts., Crimea, and E Transcaucasus.

TYPICAL EUROPEAN BEECH: small-(medium), (5)-6-10 cm long; thick-(thin); broadly elliptic/oblong, sometimes close to broadly ovate or orbicular; apex acute; acme obtuse-(acute); base (together with the very-base) rounded to cuneate; secondaries (5)-6-8-(10); margin varying from slightly serrate to slightly sinuous to slightly crenate. [Cupule traits undistinguishable from those of the Moesian beech.] Abundant in W and NW European lowlands and SE European highlands.

TURKISH BEECH: medium, (6)-8-10-(12) cm long; thick; obovate, sometimes close to elliptic; apex acute-(obtuse); acme obtuse-acute; base narrowly cuneate, with the basal margin straight then tapering into a narrowly cuneate very-base, or slightly convex when close to the very-base which is still narrowly cuneate; secondaries 8-12; margin slightly undulate to slightly sinuous; long, silky hairs densely persistent on the major veins of the lower surface. [Prominently spathulate, rounded-apexed, foliaceous, green, multi-veined appendages on the lower half of cupule-valves.] In N Anatolia (west of ca. 38 degrees W, abundant), W Anatolia, and Amanos Mts..

Two respects of features powerfully support the coherence of the five W Eurasian beech population-groups as defined above: the persistent long hairs on the major veins of the lower surface, and the overall similarity in features of cupule/nut complex (except the peculiar

cupule-appendages of the Turkish beech).

Elsewhere within the genus Fagus, persistent long hairs are present more consistently in F. japonica and F. crenata. The persistent long hairs of F. japonica are silky, whitish, very long, very slender, sometimes slightly curved or sinuous. They are mostly not very copious, but often also present on non-venal area. A few collections of the consubgeneric F. engleriana have leaves similar to the typical leaves of F. japonica in these respects. The persistent hairs of the southern populations of F. crenata are comparatively much shorter, straight, mostly not very white, generally not very abundant, and seldom present on inter-veinal area. However, the leaves of the northern populations of F. crenata approach those of F. japonica in these respects. For the beech populations in W Eurasia, the general appearance of the persistent long hairs is different from that characteristic of F. japonica and F. crenata. They are long, straight, comparatively stouter, and white. They are normally densely persistent on major veins in some populations, but they are never found on inter-veinal areas. Furthermore, because the characteristic hair of the W Eurasian beeches is stout, white, and present in high density, those persistent in primary/secondary pocket-domatia further provide these plants a very eye-attracting trait, although this kind of domatia is a characteristic of the subgenus Fagus. The populations of the Turkish beech are uniformly characterized by the typical expression of the persistent hairs. So are most populations of the Caucasian beech s.s., and the populations of Czechtz's beech growing in NW Caucasia. However, all other W Eurasian beech populations approach the southern populations of F. crenata in these respects.

Except for the prominently spatulate-foliaceous cupule-appendages of the Turkish beech, the cupule/nut complexes of all of the W Eurasian beech populations can be perceived as variants of a type of cupule/nut complex diagnostic of a rather good beech species. Such a type may be characterized by its very-long linear, drying purplish/brownish basal appendages, and prominently winged nuts that are roughly level with the large cupule-valves. A cupule/nut complex of this kind is not found in any other beech collection from outside W Eurasia. The cupules of many W Eurasian beech collections under my study are among the largest ones seen in the beeches of the subgenus *Fagus*. The range of size of cupule of the W Eurasian beeches is comparable with that of *F. longipetiolata*. Moreover, it seems evident that this feature cannot be used to define any of the five population-groups. The length of peduncle of the W Eurasian beeches is medium among the beeches of the subgenus *Fagus*. The overall variation pattern and the taxonomic usefulness of this feature are similar to the size of cupule. The hairiness of peduncle is generally correlated with that of the leaves of the same tree, as shown in all of the W Eurasian beech collections at my disposal. Four of the five population-groups growing in W Eurasia are collectively characterized by very-long linear, drying purplish/brownish basal (or lower) cupule-appendages. Within the subgenus *Engleriana*, *F. okamotoi* has drying purplish/brownish, but very-long triangular appendages. Finally, the always prominently winged nuts are among the most notable traits of the W Eurasian beeches. As indicated previously, prominently winged nuts are a derived trait within the genus. More importantly, the prominent wing cannot define any major

beech species with continuous populations, other than F. sylvatica (and F. grandifolia).

Of course, individuals "intermediate" between several of the above-defined five population-groups are found, particularly when the groups are sympatric, such as in SE Balkan, W Anatolia, Amanos Mts., Crimea, and NW Caucasia. Some of them are most probably truly evolutionarily transitional forms, such as those "intermediate" between the typical European beech and the Moesian beech in Europe, between the Caucasian beech s.s. and Czecht's beech in NW Caucasia, and between the Caucasian beech s.s. and the Moesian beech in E Transcaucasus. The "intermediacy" of this category on one hand reflects the somewhat arbitrary delimitation of the population-groups involved. On the other hand, it may imply a central position of the Caucasian beech s.s. in the evolution of the W Eurasian beech populations. The "intermediate" collections of this category are far more numerous than those of the other category under my study, which are considered as representing reciprocal genetic infiltrations between some more sharply defined population-groups.

I shall focus my study of the the evolutionary and phylogenetic relationships among these five population-groups on leaves. Based on overall gross leaf morphology, I can perceive three phenetically transitional series from among them. This work may begin with either the typical European beech or some Caucasian beech s.s., because they seem to be the most isolated populations in this respect. If the former comes first, then its closest population-group is undoubtedly the Moesian beech, which is further connected with some populations of the

Caucasian beech s.s. characterized by nearly rhombic leaves without a cordate very-base. If one begins with the most peculiar populations of the Caucasian beech s.s. with obtrullate leaves bearing a small cordate very-base, Czechtzott's beech is unquestionably nearest. Finally, the Turkish beech can be associated with the remaining populations of the Caucasian beech s.s. diagnosed by nearly obtrullate leaves with straight-margined cuneate base (and the very-base), although it is also similar to Czechtzott's beech, and to a lesser extent the Moesian beech.

At this moment, it seems clear that the Caucasian beech s.s. indeed occupies a key position in this study. The obtrullate, cordate-based, and short-petioled leaves of some populations of the Caucasian beech s.s. are not approached by any beech collection from outside Caucasia at my disposal. Only Czechtzott's beech has leaves similar to these populations. Some Caucasian beech s.s. have leaves with rather sharply serrate margin, even those on the fruiting shoots. Sharp serration to this degree is found only in the Caucasian beech s.s. among the five beech population-groups growing in W Eurasia, so far as I know. My conclusion about the relative primitiveness of clearly serrate leaf-margin, as presented in the foregoing portion of this monograph, suggests a comparatively primitive evolutionary status of the leaves of the Caucasian beech s.s..

Thus, the Caucasian beech s.s. can be regarded as very close to the most recent common ancestor of the five living beech population-groups in W Eurasia, at least in terms of the gross morphology of leaves. The Turkish beech, the Moesian beech, and Czechtzott's beech are clearly the "first-grade" living derivatives of this lineage, and the

typical European beech is most probably a "second-grade" derivative from the Moesian beech. The evolution of the leaves of the Turkish beech was accompanied by the evolution of the prominently spathulate-foliaceous, drying greenish/yellowish cupule-appendages. This sort of cupule-appendage is morphologically different from the very-long linear, drying purplish/brownish ones. However, it can only be considered to have derived from the latter, if all information from other respects, as discussed before, is taken into consideration. The leaves of the Turkish beech are evidently adapted to a drier habitat. However, I fail to perceive any selective advantage of prominently spathulate-foliaceous cupule-appendages in such habitats.

Now come the issues with Czechtzott's beech and the Moesian beech. They are sympatric in southeasternmost Balkans, Crimea, and Amanos Mts.. Czechtzott (1932: 371-372, 374-376) has briefly addressed on the ecology of the beech populations growing in Amanos Mts. and Crimea. Although beech materials from Amanos Mts. and Crimea are not abundant in the collections at my disposal, most of them are either good Czechtzott's beech or good Moesian beech. However, one good Turkish beech collection is represented in my Amanos materials: P.H. Davis 16398, (E). I have more trouble in distinguishing Czechtzott's beech from the Moesian beech in southeasternmost Europe. It is very likely that identification will become more difficult if more collections from these three sympatric regions are available.

The Amanos Mts. in SC Anatolia is well known as a "refuge" of at least pre-Pleistocene mesic plants, both woody and herbaceous ones. The rainy and cloudy mid-montane habitat there supports numerous interesting

endemics and subendemics. I follow Davis (1971: 19) in supposing a southward migration of the ancestors of these mesic plants from N Anatolia (east of ca. 40 degrees W) by way of the "Anatolian Diagonal" during the cold phase(s) of the Pleistocene, if not earlier.

The beech populations in Crimea were intensively studied in 1920s and 1930s, particularly by Poplavskaia, Vul'f, and Vul'f & Zyrina (see references cited earlier). Among the papers available to me, the one published by Vul'f in 1932 provided the latest and best summary of the studies done during this period on the Crimean beech populations. Perhaps all authors working on beeches in this period, and most later authors, included the features of the perianth-tube of male flower as critical items, if not the most important ones. However, perhaps Alden (1986: 52) is correct in commenting that "The shape and size of the male perianth lobes, often regarded as diagnostic characters, vary within the subspecies and even between the individual flowers of an inflorescence.", in his discussion on the taxonomy of the only two recognized subspecies of F. sylvatica: subsp. sylvatica and subsp. orientalis (sensu Greuter & Burdet). Among the other two important features often used by taxonomists on W Eurasian beeches: cupule-appendages and leaves, Vul'f paid particular attention to the former, after he (p. 252) found that "the dimensions and compactness of the leaf blade vary considerably in relation to the humidity and shade of their stations". Vul'f (p. 254) finally concluded that there are actually three groups of plants represented in the Crimean beech material available to him: F. sylvatica, F. orientalis, and "an intermediate form connecting these two species of beech". He provided a measurement of

the width of the lower cupule-appendages of "F. orientalis" growing in Crimea: 1-4 mm. This measurement eloquently proves the presence of beech populations with their lower cupule-appendages very similar to those typical for the Turkish beech. Among the Crimean populations regarded as of hybrid origin, Vul'f (1936: 359) reported that most of them have cupule-appendages similar to the Turkish beech.

Unfortunately, none of the Crimean beech collections at my disposal has its basal cupule-appendages broader than 1 mm. On the other hand, two Crimean collections have leaves identifiable as the Turkish beech, but have no cupule-appendages broader than 1 mm (C.S. Sargent (1903-7-13), A; Asmakhova (1957-7-27), E).

Czeczott's beech is common in NW Anatolia and the adjacent southeasternmost Balkan Peninsula. In the former area, it is sympatric with the Turkish beech; whereas in the latter area, it is probably sometimes sympatric with either the Moesian beech, or the typical European beech, or the Turkish beech. To quote Alden (1986: 52): "In Greece, especially in the northeast, some individuals resemble ssp. orientalis in vegetative characters, but never have dilated cupula scales. Such trees tend to grow at relatively low altitudes (200-1000 m), whereas typical ssp. sylvatica is mainly found in the western and central districts and rarely below 1000 m.". In my opinion, at least some, if not all, of these populations belong to Czeczott's beech, because Alden's concept on the Moesian beech is clear: "Forms often called F. moesiaca (K. Maly) Czecz., with leaves intermediate between the two subspecies,". However, the relative ecological situations among Czeczott's beech, the Moesian beech, and the Turkish beech where any two

or all three of them meet are unclear to me.

In her discussion on the beech populations growing in the Amanos Mts., Czechtott (1932: 371) was amazed by the "great variation in the dimensions of leaves". Vul'f (1932: 250) wrote: "at higher elevations the leaves were smaller, more rounded and their broadest part shifted from the upper third towards the center of the leaf;". The reduction of leaves in size with increasing elevation is also observed in Yugoslavian beech populations (Misic, 1957), as mentioned before. The interesting thing is that both of Misic's and Vul'f's works show two same tendencies in changes in dimensions of important plant organs. The first tendency is that the size of leaves reduces from lowland, through middle elevations, to highest elevations. The second is that the largest cupules (and nuts) and male flowers are found chiefly at middle elevations, whereas the size of these organs decreases with both increasing and decreasing elevations from this middle belt. The exact reason for this peculiar phenomenon is unknown to me.

The geographic distribution of Czechtott's beech and the Moesian beech is peculiar. The former is disjunct in NW Caucasia, Crimea, southeasternmost Balkan, northwesternmost Anatolia, and Amanos Mts., so far as I know. If the idea that its current populations in Amanos Mts. are derivatives of the early immigrants from NE Anatolia by way of the "Anatolian Diagonal" is adopted, then an earlier circum-Black Sea and coastal distribution pattern can be perceived. The Moesian beech is disjunct in Crimea, SE (and E) Europe, Amanos Mts., and SE Transcaucasus. In addition, a collection from NC Anatolia (A5/6; C. Tobey 782, E) has leaves morphologically intermediate between the

Turkish beech and the Moesian beech but has clearly spatulate-foliaceous cupule-appendages. This is the only specimen at my disposal that can be considered to be of hybrid origin if one wished. Thus, the geographic ranges of these two population-groups seem to be rather similar. If this phenomenon is not regarded as incidental, then an acceptable explanation may be available.

The most straightforward explanation is that these two population-groups as defined here are simply variants of one "good" population-group. If so, then such a "good" population-group should include the typical European beech on one side and embrace the Caucasian beech s.s. on the other side, because of their high degree of similarity respectively to the Moesian beech and Czechtott's beech. Consequently, one will come up with two subspecies within F. sylvatica, with the subspecies *sylvatica* incorporating two or three varieties that interfinger and/or overlap with each other in geographic ranges.

The second resolution is to regard either or both of Czechtott's beech and the Moesian beech as heterogeneous, due to the parallel development of morphologically similar populations from similar ancestral populations in different places at different or the same geologic time. Unrestricted application of this supposition may resolve many problems, and then come up with various answers to the same question. If the very likely geographic isolation between con-ancestral offspring-populations during the Pleistocene is further added into the picture, then almost any devisable explanation can be supported.

However, at least five conclusions can be drawn at this moment. First, most probably all of the living beech populations in W Eurasia

are from the same lineage. Second, the ancestral populations of this lineage were most probably already present in the Upper Miocene, if not the Middle Miocene. Third, in gross morphology, the Caucasian beech s.s. is very close to the ancestral populations of this lineage. Fourth, the very complex geological, geographic, and climatic changes occurring during and/or after the Upper Miocene have resulted in very complex variation and distribution patterns of the living populations. Fifth, even so, it is clear that insofar as the evolution of this lineage is concerned, the overall geographic direction connecting the consecutive major evolutionary events is from east (N Iran and Caucasia) to west (Balkan and Italian Peninsulas).

I am not well prepared to offer a persuasive alternative for the Pleistocene history of the five population-groups defined here. The best taxonomic treatment I can offer is to consider the Moesian beech and the typical European beech as collectively representing a western subspecies (subsp. sylvatica), and to combine the Caucasian beech s.s. and Czechtz's beech into the eastern subspecies (subsp. hohenackerana), along with a clearly defined central subspecies: subsp. orientalis.

3-6 SECTIONS OF THE SUBGENUS FAGUS: SECTION GRANDIFOLIA SHEN, SECT.NOV.

A diagnosis of this section within the subgenus has been offered in the synoptical key to subgenera and sections (see 2-3). A synoptical key to the subspecies of the single species of this section: F. grandifolia, is given as follows.

1A.LEAVES generally oblong/elliptic, sometimes with a clearly cordate
BASE. MARGIN generally slightly serrate, sometimes with nearly
straight SINUSES. LOWER SURFACE normally densely covered with short,
white, eglandular hairs. AREOLES normally prominently elevated.
CUPULE-VALVES generally ovate and with an obtuse apex, usually
rufous. CUPULE-APPENDAGES relatively short, typically ca. 2-4 mm
long. SE UNITED STATES (Atlantic Coastal Plain & Gulf Coastal Plain).

3-6b F. grandifolia subsp. caroliniana

1B.LEAVES normally without a clearly cordate BASE. LOWER SURFACE
generally without short, eglandular hairs, but with abundant
persistent tiny, yellow, glandular hairs instead. CUPULE-VALVES
generally narrowly triangular and with an acute apex, usually grayish
yellow.

2A.LEAVES generally (broadly) ovate to nearly (broadly) rhombic.
MARGIN generally serrate. AREOLES normally prominently elevated.
CUPULE-APPENDAGES relatively long, typically ca. 4-8 mm long.
APPALACHIAN MTS., north to NOVA SCOTIA & PRINCE EDWARD ISLAND of
Canada.

3-6a F. grandifolia subsp. grandifolia

2B.LEAVES generally lanceolate to nearly (narrowly) trullate. MARGIN
generally slightly serrate, sometimes with nearly straight SINUSES.
AREOLES normally slightly elevated. CUPULE-APPENDAGES relatively
short, typically ca. 2-5 mm long. E MEXICO.

3-6c F. grandifolia subsp. mexicana

Fagus grandifolia Ehrh., (1788), Beytr. Naturk. 3: 22-23. [No collections cited; no figures offered]

Fagus grandifolia Ehrh. subsp. grandifolia

Fagus heterophylla Raf., (1838), New Fl. N. Amer.: 80.

Fagus grandifolia Ehrh. subsp. caroliniana (Loudon) Camp ex Shen, comb. nov.

Fagus ferruginea Aiton var. caroliniana Loudon, (1838), Arb. Frut. Brit. 3: 1980, fig. 1915. [No collections cited]

Fagus grandifolia Ehrh. var. caroliniana (Loudon) Fernald & Rehder, (1907 July), Rhodora 9(103): 114. [No collections cited]

"Fagus Americana latifolia" Muenchhausen, (1770), Hausvater 5: 162.

Fagus ferruginea Aiton, (1789), Hort. Kew. 3: 362.

Fagus sylvestris Michaux, (1803), Fl. Bor.-Amer. 2: 194.

Fagus grandifolia Ehrh. subsp. mexicana (Martinez) Camp ex Shen, comb. nov.

Fagus mexicana Martinez, (1940), Anal. Inst. Biol., Univ. Nac. Aut. Mex. 11(1): 85-87. [No collections cited]

Fagus grandifolia Ehrh. var. mexicana (Martinez) Little, (1965 Sept), Castanea 30(3): 168.

LARGE DECIDUOUS TREES, to 40 m tall, 1.5 m DBH. BARK smooth, generally silvery/whitish, sometimes with shallow vertical fissures, or

speckled with tiny rice-grain-like lenticels. **CURRENT-YEAR SHOOTS** purplish/brownish, normally more than 1 mm thick, sometimes covered with persistent whitish long hairs. **BUDS** sessile, ovoid when short, fusiform when longer than ca. 3 mm, bud-scales usually only inconspicuously hairy on the uppermost margin. **LEAF-UNFOLDING** in middle April (in the south) to early May (in the north). **LEAVES** broader in subsp. grandifolia and subsp. caroliniana, narrower in subsp. mexicana; generally ovate to nearly rhombic (in subsp. grandifolia), normally oblong/elliptic, sometimes oblong/obovate (in subsp. caroliniana), lanceolate to nearly trullate (in subsp. mexicana); thick- to thin-chartaceous (in subsp. grandifolia and subsp. caroliniana), generally thin-chartaceous (in subsp. mexicana). **APEX** normally acuminate to acute, always with a narrow and long ACME. **BASE** generally cuneate to rounded, but often cordate in subsp. caroliniana. **UPPER SURFACE** dark-green, particularly so in subsp. caroliniana. **LOWER SURFACE** light-green; sometimes slightly glaucous in subsp. caroliniana and subsp. mexicana; normally with persistent long, whitish hairs on the major veins; in subsp. caroliniana normally with short, whitish, eglandular hairs in the intervein areas; in subsp. grandifolia and subsp. mexicana usually with abundant tiny, yellowish, glandular hairs on the whole surface. **SECONDARIES** 12-18-((22)); always each terminating in a tooth-tip. Primary/secondary **POCKET-DOMATIA** always present. **MARGIN** serrate to slightly serrate (in subsp. grandifolia), slightly serrate and sometimes with nearly straight sinuses (in subsp. caroliniana and subsp. mexicana). **PETIOLE** generally very short, ca. 1/10-1/15 as long as the leaf-blade.

The flowers per **MALE INFLORESCENCE** ca. 15-31-(40). The hairs on

the upper portion of the PERIANTH-TUBE whitish. FRUIT MATURING in July. CUPULE-PEDUNCLE generally 8-20 mm long; hairy to glabrous. CUPULE-VALVES generally ovate, with an obtuse apex and rufous (in subsp. caroliniana), or generally narrowly triangular, with an acute apex and grayish yellow (in subsp. grandifolia and subsp. mexicana). CUPULE-APPENDAGES nearly always fused with the cupule-valve for a considerable distance, except for the rarely occurring spatulate-foliaceous, multi-veined, drying greenish/yellowish basalmost ones that are very few when present (in all of the three subspecies); linear, 4-8-((10)) mm long and generally spreading (in subsp. grandifolia), subular/linear, ca. 2-4-((5)) mm long and generally departing from the cupule-valve at an angle of ca. 80-120 degrees (in subsp. caroliniana and subsp. mexicana); sometimes arranged in discernible horizontal rows (in subsp. caroliniana only). NUTS ovate to broadly ovate, sometimes nearly triangular; always with about 3 vertical ridges on each surface; always with normally prominent wings along the whole length (to the very base); generally roughly level with the cupule-valves (in subsp. caroliniana and subsp. mexicana), or often well exserted from the cupule-valves (in subsp. grandifolia). E NORTH AMERICA (from Nova Scotia and Prince Edward Island south to southern Appalachians [subsp. grandifolia], Atlantic Coastal Plain to Gulf Coastal Plain [subsp. caroliniana], disjunct within Mexico (Tamaulipas, Hidalgo, Puebla, and Veracruz) [subsp. mexicana]).

LECTOTYPIFICATION OF SUBSP. GRANDIFOLIA:

This subspecies is the so-called northern form or northern

variety of the North American beech, in the common concept of the botanists of the United States and Canada. The vernacular name "gray beech" has long been used by the general public and (local) foresters living or working in the northern lowland region to refer to their beech. This common name is here regarded as adequate for this northern entity, as has been done by many taxonomists since the last century.

F. Ehrhart proposed a specific epithet grandifolia for a single tree cultivated somewhere in Europe in 1788. This name was buried in literature until Rehder relocated it and applied it to the American beech populations, to replace the then most common name of the American beech: F. ferruginea, in 1907, following the Vienna Code. [W. Aiton published the name F. ferruginea in 1789.] However, Rehder had only one remark to support his judgment on the identity of F. grandifolia:

"Ehrhart's F. grandifolia represents apparently the northern form."

Rehder had not seen any specimen collected from the tree on which Ehrhart had based his name. Unfortunately, I do not know who knows where this tree is. To quote Rehder (1907: 112): "By this nomenclatorial change we avoid the rather awkward situation that a very rare form should constitute the type of this widely distributed American tree, for F. ferruginea Aiton is apparently based on one of the hitherto almost unknown pubescent forms of the Beech.". Rehder further considered another three earlier names ("F. americana latifolia Muenchhausen, 1770; F. sylvatica var. americana latifolia Duroi, 1771; F. ferruginea Aiton, 1789) to have referred to the northern form. They were all based on cultivated individuals in Europe. His arguments supporting this decision were neither very clear nor very convincing.

Most probably Rehder had also never seen any specimen nomenclaturally associated with these three names. However, in my opinion, the name F. grandifolia is ambiguous at subspecific level, like most of the names proposed for the American beech, and both Muenchhausen's "F. americana latifolia" and Aiton's F. ferruginea are referable to the southern form of the American beech.

The name F. grandifolia has been consistently and persistently applied to the North American beech populations (growing in the United States and Canada) as a whole for almost a century. It is certainly an adequate name at specific level under any considerations. The real trouble is its subspecific identity, as stated above. However, its history of being applied to the northern entity is almost as long as the history of its constant application to the North American beech as a whole. I see no need to argue further its subspecific identity.

The final problem left here is lectotypification. The several earliest names (incl. F. grandifolia) of the North American beech were all proposed by European authors, based on cultivated trees. No collections nomenclaturally associated with these names were available for me, although there are such. Judging from the original descriptions, only a later name F. heterophylla Raf. (1838) is here assigned as synonym of subsp. grandifolia. Based on my study, the collections from the general region roughly east of 75 degrees W and north of 43 degrees N are rather "pure" members of the northern entity. In other words, plants congruent with my description and/or growing in Vermont, New Hampshire, Maine, Quebec, New Brunswick, Nova Scotia, or Prince Edward Island, may be taken as typical individuals of subsp.

grandifolia, and they are thus called "typical gray beech".

No lectotypification is undertaken here.

The species F. grandifolia as defined here will be mentioned hereafter by the name the "American beech" or "North American beech".

The specific epithet "grandifolia" properly reflects the European impression of the leaves of the American beech. The average size of the leaves of the American beech is in fact comparable with that of F. japonica, F. engleriana, F. longipetiolata, and F. sylvatica subsp. hohenackeriana.

LECTOTYPIFICATION OF SUBSP. CAROLINIANA:

According to the most common local usage, the name white beech refers to the plants growing in the southeastern coastal plain, and the name red beech is used for those thriving in the Piedmont and mid-mountains of the Appalachian Plateau. Both of these two vernacular names had been applied to intermediate populations growing in intermediate area by a few important authors. However, the name "white beech" is adequate as the common name of this subspecies, because the most typical populations of subsp. caroliniana can only be found in southeastern coastal plain.

No collections had been cited when G. Loddiges first proposed the name F. caroliniana in 1826 (a nomen nudum), J. C. Loudon made his combination F. ferruginea var. caroliniana in 1838, or Fernald & Rehder published their transfer F. grandifolia var. caroliniana in 1907. No collections associated with these names (in any sense) were available for my investigations.

Based on my study, collections from the southern Atlantic Coastal Plain (south of ca. 36 degrees N) and eastern Gulf Coastal Plain (south of ca. 33 degrees N) are "pure" individuals of the southern entity. In other words, plants congruent with my description and growing in lowland North Carolina, South Carolina, Georgia, Florida, Alabama, Mississippi, Louisiana, and E Texas may be regarded as typical subsp. caroliniana, and they will be called the "typical white beech" hereafter.

No lectotypification is presented here.

LECTOTYPIFICATION OF SUBSP. MEXICANA:

LECTOTYPE: M. Martínez 1500, MEXICO, Hidalgo-Zacualtipan; MEXU-9631 !
Lectotypified by Fox & Sharp, in 1954, in Bol. Soc. Bot. Mex. 17: 31;
for F. mexicana.

M. Martínez did not cite any collection in his original description of F. mexicana. He had mailed and brought some specimens to some American taxonomists before he submitted his manuscript describing his new species in 1940 January. Fox & Sharp (1954) indicated the collection M. Martínez 1500 (collected in July 1939) as the type.

Many Martínez collections are at my disposal. They seem to be from a very small region, if not the same local population, judging from the field-notes about the locality and the appearance of the specimens. Flowering branchlets and those with over-mature fruits are often present on the same sheet. The collection numbers and dates, when present, are very confusing. Thus, specimens from different herbaria are hard to correlate. Those collected before 1940 are as follows: Martínez 800 (1939 June; US-1749597), Martínez 1500 (1939 July; MEXU-9631), Martínez

s.n. (1939-9) (A). R. Hernandez Magana annotated the MEXU specimen as the type of F. mexicana, in 1987.

I consider Fox & Sharp had properly lectotypified the name F. mexicana, in 1954.

This subspecies is confined to Mexico, and will be designated the "Mexican beech".

ILLUSTRATIONS:

Subsp. grandifolia: Hosie (1979: 177), etc.

Subsp. caroliniana: Radford et al. (1968: 371), Duncan & Duncan (1988: 151), etc.

Subsp. mexicana: Martinez (1940: 86).

DISTRIBUTION AND ECOLOGY:

In E North America, subsp. grandifolia and subsp. caroliniana have a collective geographic range east of the midwest prairie and farming belt, and south of the boreal forest belt (composed mainly of evergreen pinaceous conifers). Roughly speaking, these two subspecies have occupied all land-areas (in E North America) whose climatic conditions can support the growth of an "average" beech. In their southwesternmost range, they are limited by the dry climate. In their southeasternmost range, the poorly drained soils restrict their growth. In their northeasternmost range, they have reached the boundary between the Northern Hardwood Forest and the Boreal Coniferous Forest. The highly continental climate in western Great Lakes Region is too hostile for any living beech species.

The genetic mixture between subsp. grandifolia and subsp. caroliniana is amazing. The "purest" populations of subsp. grandifolia are found at the highest elevations of southern Appalachians, and the general region north of southern New England and east of the Great Lakes Region. The "purest" populations of subsp. caroliniana grow in southern Atlantic Coastal Plain and Gulf Coastal Plain. The various climatic regimes in mid-elevational montane and plateau region foster the growth of populations exhibiting various combinations of pertinent taxonomic traits of the two subspecies. [Unfortunately, perhaps most of the names proposed for the North American beech (in the United States and Canada) were based on trees growing in this very broad transitional region.] I have discussed the possible climatic reason for the prevailing N-S trending distribution pattern of the major forest-trees in E North America, in 3-5. This phenomenon is also definitely associated with the N-S oriented Appalachian Mts., which is on the average higher in its southern portion and lower to the north.

In this connection, it should be borne in mind that even the highest peaks in southern Appalachians are only about 1,800 m. The (nearly) continuous populations of F. crenata, F. sylvatica subsp. hohenackeriana, and F. sylvatica subsp. orientalis, in contrast, may appear from sea-level to over 2,000 m within a rather narrow latitudinal belt, which is no more than 500 km in N-S stretch, without showing appreciable morphological differentiation. These two subspecies of F. grandifolia can be reasonably supposed to have existed before the Pleistocene. The ancestral populations of subsp. caroliniana would have been distributed along the coastal plain by that time; and those of

subsp. grandifolia would have already assumed a northern lowland and/or southern Appalachian distribution pattern. Judging from the gross morphology of the "purest" populations of each of these two present-day subspecies, the taxonomic distance between their pre-Pleistocene ancestral populations was most probably no greater than that between two or three subspecies of any other living beech species. The chiefly N-S oriented range expansion and contraction during the Pleistocene would have caused a tremendous amount of mixed populations even hundreds of thousands of years before, given that the genetical and physiological isolation between the two original subspecies was not sufficiently effective to prevent successful hybridization at that time. Back-crossing and introgression must have occurred subsequently and concomitantly. Thus, during interglacials (and very warm interstadials), various genetically intermediate populations might have gradually encroached into the previously unoccupied habitats, if any, that had "functioned" as a geographic and/or ecological isolating factors between the two pre-Pleistocene subspecies. A further "back-encroachment" into the habitats that were originally well inhabited by the two ancestral subspecies is also possible, at least due to the hybrid vigor. Another very possible situation is that the more and more stronger southward climatic forcing (the frequent visit of strong winter-chills) would have created more and more "good" habitats for the naturally selected, genetically intermediate populations to the south. [Consequently and concomitantly, there might be a turning-point belt in terms of those differentiating features, rather than smoothly shifting parallel intergrading lines. Moreover, such a belt might be

comparatively rather close to the northern limit of the "purest" populations of the white beech.] The fact that the genetically intermediate populations nowadays occupy a range that is longer N-S than W-E may reflect the various ecological consequences of this climatic forcing. The resultant lax competitive environment must have also "helped" these mixed beech populations encroach into some habitats previously chiefly inhabited by other plants, during the Pleistocene. The current "pure" populations of subsp. grandifolia are present well beyond the limit of the greatest extension of the last strongest continental glaciation; whereas the current habitats of the "pure" populations of subsp. caroliniana are just where the most important "refuges" of mesic and more cold-hardy plants had located, so far as I know. The combined range incorporating the ranges of "pure" gray beech, mixed beech populations, and "pure" white beech is thus conspicuously N-S trended.

The above discussion could explain the highly "intermediate" beech populations found all over the "most visited" habitats of the North American beech (in the United States and Canada). Whether or not this model is also applicable to other important E North American tree-species is unclear to me.

Naturally occurring beech populations can be found all over the geographic range of the species in the United States and Canada. The most extensive and beautiful forests containing beech as a co-dominant species are found chiefly in New York, Ontario Peninsula, W Pennsylvania, N Ohio, and southern Appalachians. Except the last region, all of the important habitats are within the limit of the greatest extension of the

last strongest continental glaciation. I believe that the vast majority, if not all, of the beech populations flourishing in these regions (incl. the southern Appalachians) are of variously mixed origin. And it is their hybrid origin that gives them such a superior performance in the middle two thirds of the N-S oriented range of the species, relative to those "pure" populations in the northernmost and southernmost ranges respectively.

The gray beech is famous for its vigorous sprouting ability. Beech stands densely beset with root-sprouts are common in northern lowlands. According to Held (1983: 55), "... , root sprouting is considered by many researchers to be the main mode of reproduction in this species in certain areas of its range." Like perhaps all other beech species, the American beech is slow-growing and long-lived. The Canadian beech populations are the most shade-tolerant among their major forest-associates, as the Canadian populations of Tsuga canadensis are among their major coniferous companions (Logan, 1973).

The overall ecological adaptation of the typical white beech is somewhat similar to that of the northern group of F. longipetiolata. The typical gray beech is approached by the most cold-tolerant populations of F. crenata subsp. crenata and F. engleriana in this respect. I do not consider the overall ecological adaptation of the typical white beech to be significantly different from that of its pre-Pleistocene ancestor. As to the typical gray beech, the major climatic changes that had occurred in the Pleistocene E North America must have modified its ecological traits.

The Mexican beech is disjunct in Mexico. The northernmost

Mexican locality (in Tamaulipas) is about 900 km south of the southernmost Texas locality for subsp. caroliniana. There are five known localities of the Mexican beech. They are in Tamaulipas (1; ca. 23 degrees N), Hidalgo (2), Puebla (1), and Veracruz (1; ca. 20 degrees N), from north to south (see Fox & Sharp, 1954). All of these five montane localities are situated on the eastern escarpment, or within the major divide region, of the Sierra Madre Oriental. The general climate of these habitats is similar to that prevailing in the southern Appalachians, but has more growing-season rainfall and higher winter temperature-extremes. Collectively these sites are in the northern portion of the series of "relic" habitats of the Tertiary Mixed Mesophytic Forest south of the United States. These highly humid and cloudy (foggy) northern "relic" habitats maintain beautiful American MMF, that is supposed to have gradually succeeded the Middle Miocene Notophyllous Evergreen Broad-leaved Forest, during the Upper Miocene. The total area of these northern habitats is rather small, but the diversity of the MMF-associated woody flora at least at generic level is roughly comparable with the present-day MMF preserved in the E United States. In addition to the overall similarity between these two "relic" floras at generic level, a taxonomic identity of the counterparts at specific level has often been assumed. The validity of such an assumption warrents a careful reconsideration. For references in the phytogeography and ecology of these habitats, see Miranda & Sharp (1950), Hernandez-X. et al. (1951), Rzedowski (1978), among others.

The Mexican beech populations are mostly present as almost pure stands on (very) steep rocky slopes from 1,500 m (in the north) to 1,900

m (in the south). The latitudinal location, altitudinal range, and general climatic conditions of the habitats of the Mexican beech forest, as well as the ecological niche of the Mexican beech, are roughly comparable with those of F. hayatae subsp. hayatae in N Taiwan, except that Tsuga is unknown in Mexico.

Based on my earlier discussion on the comparative ecology of the East Asian beeches, the Mexican beech appears to be more advanced along the general and "normal" route of temperature-adaptation than the typical white beech, under a sufficiently mesic and "normally" competitive environment. Since a drier climate in S Texas and NE Mexico developed during the Upper Miocene, the geographic isolation of the ancestral populations of the Mexican beech from those of the typical white beech may be supposed to have been rather effective no later than the end of the Upper Miocene. Thus, the further evolution of the Mexican beech in ecological adaptation may be supposed to have occurred during the Pliocene and Pleistocene. If so, the American beech will provide a demonstration of the ecological evolution of beech during the past several millions of years.

TAXONOMIC REMARKS:

The beech populations growing in the United States and Canada have long been regarded as belonging to a single species by American botanists. As seen in textbooks, the name F. ferruginea had dominated the nineteenth century, and the name F. grandifolia has been consistently used within the 20th century. It seems that the extreme variability of the American beech in gross morphology has defeated the

great efforts of some taxonomists for a "good taxonomy" of the American beech, while it has on the other hand almost always functioned effectively in maintaining the American beech as a single species in the mind of most taxonomists.

Adam Zajdel had finished a Master's thesis in 1942 under the direction of W. H. Camp. About two thirds of the pages were devoted to a "Historical Development of Our Understanding of the North American beech". He finally offered a very long list of synonyms and important applications for each of the two recognized species (F. alba = the southern form, F. grandifolia = the northern form), also based on literature research, as Rehder had done in 1907. Comparison of Rehder's and Zajdel's lists of synonyms shows some names under different entities (northern or southern). Only a few of the treatments discussed or mentioned by Zajdel are here considered to refer unambiguously to either of the two entities, for two reasons. First, the two entities are so genetically mixed in such a wide area that most of the populations considered in the vast majority of the early taxonomic works are not genetically "pure" and thus not readily recognizable in the literature. Second, the general manner of expression of most of the earlier descriptions is, as a rule of that period, too simple and vague to cope with the high degree of variability of the American beech. Hence, it is customary that I cannot tell whether the populations on which a description was based belong to the typical gray beech, mixed populations, or the typical white beech.

Within this century, five American taxonomists have tried to reach a satisfactory taxonomy of the American beech. The first of them

is A. Rehder (1907). He took the first validly published specific name F. grandifolia Ehrh. (1788) to replace the traditionally most commonly applied name F. ferruginea Aiton (1789), for the American beech, following the Vienna Code. He simultaneously well perceived the existence of two basic forms within the American beech: a northern one and a southern one. [The existence of beech in Mexico was unknown to the scientific field until 1939 when it was first collected, and 1940 when it was described.] Along with a conviction that the name F. grandifolia refers to his northern form, Rehder then adopted Loudon's epithet caroliniana to accommodate his southern form as var. caroliniana. All of these conclusions have been followed by the subsequent authors and the botanical public till now, except for Camp, and to a lesser extent his student Zajdel.

The second name appearing in the scene is W. H. Camp. In late 1930s, he was attracted by the extreme variability of the American beech. After he had done some work intermittently during the subsequent several years, Camp transferred this project to his student A. Zajdel. Zajdel, as the third person who had done much on the American beech, submitted his Master's thesis in 1942. Camp resumed this project after the Second World War. He lectured frequently on his most recent results, and corresponded with dozens of people, both professional botanists and amateurs, for consultation, discussion, or help in any sense, during 1940s and 1950s. He left several handwritten drafts, typescripts, and finished plates (prepared by C. L. Gilly), on several major beech species in East Asia, W Eurasia, and North America. All these documents are now preserved in the archives of the New York

Botanical Garden, where he worked from the early 1930s till 1950. At least one thousand of beech specimens were annotated, most of them being the American beech. More than 10,000 individuals of the American beech had been sampled for measuring morphological variation (see Camp, 1961: 55). Unfortunately, his great project of writing a monograph of the genus Fagus was never completed. The only publications are a 126-word abstract (Camp, 1940), a three-page abstract (Camp, 1951), and a short-paragraph (Camp, 1961), before his untimely death (in 1963). All three deal with the American beech.

Camp first approached the American beech issue based on Rehder's concept and nomenclature. He (Camp, 1940 Dec) reported that the American beech was derived from the "intermingling of at least two quite distinct specific entities". In his archive, I found a synoptical key and a set of finished line-drawings, both depicting his concept of 18 species within the genus. Five of them refer to the beech populations growing in Canada, the United States, and Mexico. Judging from his correspondence, he came up with these no later than early 1941. At about the same time (perhaps a bit earlier), Camp found that Rafinesque is interesting. Rafinesque had achieved five specific names to accommodate the American beech by 1838: F. alba Raf., F. ferruginea Aiton, F. heterophylla Raf., F. rotundifolia Raf., and F. nigra Raf.. For the beech populations growing in the same geographic region, Camp had four specific names: F. grandifolia Ehrh., F. heterophylla Raf., F. rotundifolia Raf., and a species using the epithet jennisoniana. In his 1951 paper (an abstract), Camp clearly presented his concept on the origin of the American beech growing north of Mexico. He perceived a

genetical blending among the three "distinct" pre-Pleistocene American beech "species" (white beech, red beech, and gray beech) during the Pleistocene, and did not consider the argument on taxonomic treatment of the living populations to be very meaningful in the biological sense. In 1954 January, Camp prepared a "key to the subspecies of Fagus grandifolia in North America". In this unpublished key, there are four subspecies under the epithets: caroliniana (white beech), ferruginea (red beech), heterophylla (gray beech), and grandifolia (common beech). The most important concept Camp brought out then is: "Because of the intergrading nature of subspecies, ssp. grandifolia functions primarily as a nomenclatural vehicle for those stands and individual trees which do not fit well into any of the three basic subspecies.". In the same year, Camp annotated many specimens of the American beech based on his concept of five subspecies (incl. subsp. mexicana, in addition to the above-mentioned four). Neither his evolutionary concept nor his taxonomic treatment was published after 1951. According to Rupert Barneby (oral comm., 1991 July), Camp finally seemed to have come up with an idea that all living beech populations could be perceived as representing a single species. This perhaps may explain at least in part why Camp never finished his monograph of the genus Fagus.

The Camp legacy for the botanical public is his 1951 paper. It has always been cited in subsequent literature addressing the taxonomy of the American beech, although Camp's contention on the three distinct and good entities has never been followed.

Zajdel (1942) had two species to accommodate the beech populations growing north of Mexico: F. grandifolia Ehrh. and F. alba

Raf.. Being influenced by Camp, admittedly, he seriously considered the hybridization problem, and listed four names as possibly representing mixed populations: F. ferruginea Aiton (1789), F. nigra Raf. (1833), F. grandifolia forma pubescens Fernald & Rehder (1907), and F. grandifolia var. pubescens Fernald & Rehder (1935).

Mercer (1975) finished a Master's thesis on the morphological variation of beech populations in North Carolina. Cooper & Mercer (1977) published a paper on the same subject. Their morphometric and statistical analyses on dozens of population-samples collected from all over North Carolina allowed them to support the presence of only two entities growing in North Carolina, which was among the most intensively studied areas of Camp.

Now comes my approach and appreciation on the American beech problem. First, no hybridization has been recognized among the three Chinese beech species of the subgenus *Fagus*, based on my own and Y.-T. Chang's observations. [Chang is the author of the genus Fagus of the Flora of China, the Fagaceae of which has not yet published.] The two subspecies of F. crenata do not show an extensive transitional region. Second, within F. sylvatica, the known hybridization between the clearly defined subsp. orientalis and the other two subspecies is not abundant. Third, my own observation shows that there are indeed two sufficiently good entities of the North American beech growing north of Mexico. They are found only in the northernmost and the southernmost ranges respectively. The middle two thirds or one half of the range is inhabited by variously morphologically intermediate populations. Fourth, the taxonomic distance between these two entities is roughly

comparable with those between (or among) the subspecies of all other living beech species treated before. Thus, all of the North American beech populations growing north of Mexico should be considered to belong to a single species. Following the common usage and the Code, the name F. grandifolia is applied to all of the North American beech populations growing north of Mexico. Fifth, the definition of my northern entity is close to those of Rehder's northern form (see Rehder, 1907), Camp's gray beech (Camp, 1951; and his unpublished later works, particularly his 1954 key), and Zajdel's F. grandifolia Ehrh. (Zajdel, 1942). On the other hand, my southern entity is similar to Rehder's southern form, Camp's white beech, and Zajdel's concept of F. alba Raf.. Sixth (and finally), I do think that the taxonomic recognition of two major infraspecific entities (to accommodate my two entities) is useful and reasonable, however rampant the hybridization between them is. The sharp observation of the existence of two population-groups, first presented by Michaux in 1803 and 1811, and subsequently adopted by Rehder (and Fernald) in 1907, is thus well appreciated. I thus treat my northern entity as the nomenclaturally typical subspecies, and my southern entity as subsp. caroliniana. This is chiefly because the beech populations growing on the southeastern coastal plain have a fairly clear taxonomic history since the very beginning of the history of the botanical research of the American beech (see my synonym list for subsp. caroliniana). Furthermore, the simultaneous application of the epithet grandifolia to the northern populations and the epithet caroliniana to the southern populations (since 1907) has stabilized the connotation of these two epithets. However, I am not sure about the

actual infraspecific identity of the type tree of the epithet grandifolia: my northern entity, my southern entity, or of mixed origin.

Camp's red beech actually represents mixed populations, based on his synoptical key (1954 Jan, unpubl.), and the distribution and ecology provided by Camp (1951; 1954 Jan, unpubl.). Camp paid much attention to the acidity of the soils of the beech habitat in his taxonomic concept. This edaphic feature is indeed important in the taxonomy of Vaccinium, Camp's specialty, but it is not important for the growth of beech as a whole, according to our current knowledge. The ranges in soil acidity Camp had reported for his white beech, red beech, and gray beech respectively are just collectively well within the range value common and normal for various beech taxa. Camp also emphasized the shapes of male flower and its segments in his taxonomy of all living beeches. The instability of this feature in European beeches is well documented by Alden (1986: 52).

Now comes the Mexican beech. After the first collection in 1939 made by M. Martinez, five localities are so far known. About 20 collections are available to me. The variation in gross morphology among populations from different localities is not very prominent. Among the beech collections at my disposal, no Mexican collection is similar to any collection from the United States or Canada to the extent that it can be safely assigned into either of the two above-mentioned subspecies or considered to be of mixed origin between them. On the other hand, the following traits of the Mexican plants collectively well and exclusively fit the concept of the species F. grandifolia (composed of two subspecies as stated above): very short petiole; very numerous

secondary veins; on the average slightly serrate leaf-margin; acute to acuminate apex, with caudate or narrowly acute acme; ovate, broadly ovate, to nearly triangular nuts, which are level with or slightly exserted from the cupule-valves, and with prominent wings from the top to the very base; medium-sized cupule atop a short- to medium-long peduncle; at most short linear cupule-appendages, at least occasionally occurred prominently spathulate-foliaceous, drying greenish/yellowish, multi-veined basalmost appendages.

The leaves of the Mexican plants are rather narrow. Similarly narrow leaves are only approached by occasional populations growing north of Mexico. They are very thin, long-ovate to lanceolate on sterile and shade shoots. Those growing on fertile shoots are slightly thicker and nearly trullate to trullate. Lanceolate or trullate leaves are never found in beech collections from north of Mexico. On the other hand, the diagnostic nearly rhombic leaves of the typical gray beech, or the characteristic obovate/oblong leaves of the typical white beech are never found in beech collections from Mexico. Glandular hairs are abundant on the inter-veinal area of the lower leaf-surface of the Mexican plants. This trait also characterizes the typical gray beech. The leaf-margin of the Mexican plants has a range of variation comparable with that of the typical white beech. The cupule-valves of the Mexican plants are narrowly triangular and thus similar to those of the typical gray beech; whereas their cupule-appendages are normally short, subulate/linear, and at least not spreading like those of the typical gray beech, they are thus closer to the typical white beech. As a conclusion, it is clear that the Mexican plants collectively represent

a "new" and well marked subspecies of F. grandifolia as defined above. The relative distinctions among the three subspecies are roughly similar. Nevertheless, it may be perceived that subsp. mexicana is phenetically somewhat closer to subsp. grandifolia than to subsp. caroliniana, although subsp. caroliniana is geographically much closer to subsp. mexicana than subsp. grandifolia is.

[An admirable morphometric and statistical research on the North American Carpinus caroliniana complex was conducted by Furlow (1987a; 1987b). He came up with a taxonomy with two species each comprising two subspecies. The geographic range of Carpinus caroliniana is very similar to that of Fagus grandifolia north of Mexico. So is the range of Carpinus subsp. caroliniana to that of Fagus grandifolia subsp. caroliniana (Furlow, 1987b: Fig. 2, 3). However, the northern subspecies of Carpinus caroliniana: subsp. virginiana, is considered to have its "pure" populations extend well southward into the region where I think no sufficiently "pure" populations of F. grandifolia subsp. caroliniana occurs. Subspecies mexicana of Carpinus tropicalis is found in "pure" form scattered along the eastern escarpment of the Sierra Madre orientale and the southern margin of the Mexican Plateau. "Pure" populations of subsp. tropicalis of Carpinus tropicalis are centered south of the range of "pure" subsp. mexicana, southward to N Nicaragua. Thus, the overall situation of distribution of the four major entities of the Carpinus caroliniana complex is comparable with that of the three subspecies of Fagus grandifolia. For clarity, I here list the four taxa of the Carpinus caroliniana complex from north to south as follows: subsp. virginiana, subsp. caroliniana, subsp. mexicana, subsp.

tropicalis.

Now is the turn of the comparison in gross morphology among the four major entities of the Carpinus caroliniana complex. Furlow provided good line-drawings of these four taxa (Furlow, 1987b: Fig. 1, 4). It is readily perceptible by examining these illustrations that the two entities north of Mexico belong to a higher-level entity, and the two entities south of the United States evidently have a most recent common ancestor that is a sibling group of another lineage that had led to the two northern entities in the geological past. This observation is based on the overall and exclusive similarity between the two members of each pair of taxa in the gross morphology of staminate inflorescence and infructescence bract, and is concordant with Furlow's taxonomic treatment. As to the leaves, it is clear that subsp. virginiana (oblong, apex acuminate, base rounded, larger, secondaries medially numerous) is far more similar to subsp. mexicana (oblong/ovate, apex acuminate, base cordate, larger, secondaries medially numerous) than to the remaining two taxa, and vice-versa. The leaves of subsp. caroliniana (elliptic/ovate, apex acute, base rounded, smaller, secondaries least numerous) seem to be roughly equidistant from subsp. virginiana and subsp. mexicana. Subspecies tropicalis has leaves narrowly oblong to lanceolate, apex acute to acuminate, base cuneate, larger, secondaries most numerous. They are slightly closer to the leaves of subsp. virginiana than to those of subsp. mexicana. The table of "salient quantitative morphological characters" of the four taxa provided by Furlow (1987b: 417) clearly indicates a very isolated position of subsp. caroliniana, as shown by its unique possession of

large capitate glands on leaves and unique lack of division in filament. Both features are critical in the taxonomy of Betulaceae. I have no intention here to argue for any idea about the evolution of the four entities of the Carpinus caroliniana complex. However, this example may help us to appreciate how complex this kind of problem could be, and be instructive in our understanding of the problem with Fagus grandifolia.]

Fagus grandifolia is characterized by the very numerous lateral veins of its leaves. This is a primitive trait within the genus, as remarkably demonstrated by F. sylvatica. The often sharply serrate margin of the leaves of subsp. grandifolia most probably represents a plesiomorphy of the genus, judged from the living taxa. The evolution of the leaves of the three subspecies of F. grandifolia is difficult to discuss without the proper reference of other beech taxa. I also cannot perceive the selective advantages of the various evolutionary changes in the leaves of F. grandifolia in association with either the current climate or the supposed past climate, except for the very thin leaves of the Mexican beech if they are derived. Nevertheless, I shall comment on the leaves of the American beech as follows:

First, the commonly seen nearly rhombic leaves of subsp. grandifolia must have derived from the ovate ones, which are also normal for the typical gray beech. Hence, the evolution of leaf-shape is similar in F. grandifolia subsp. grandifolia and F. crenata.

Second, the obovate/oblong leaves of subsp. caroliniana must have derived from the elliptic/oblong ones, which are also normal for the typical white beech. Therefore, the evolution of leaf-shape of F. grandifolia subsp. caroliniana is comparable with that of F. hayatae.

Third, the leaves on sterile shoots of subsp. mexicana are very similar to those on sterile shoots of F. brevipetiolata in texture, size, shape, apex, base, margin, number of secondaries, and length of petiole. Resemblance to this degree is really amazing. The difference between them resides in trichomes. Fagus brevipetiolata seems to lack tiny, yellowish, glandular hairs on lower leaf-surface. This sort of trichome is found in all other beech taxa so far examined, and is particularly abundant in the Mexican beech. There is no reason to suppose the lack of this kind of trichome in F. brevipetiolata to be plesiomorphic within the genus. The other basic leaf-shape of subsp. mexicana, (nearly) trullate, is typical for the leaves on fertile and/or sunny shoots. Trullate leaves are elsewhere seen in the southern group of F. longipetiolata, F. lucida, and F. hayatae subsp. hayatae.

Fourth, more similarities in leaf features between the two sections Grandifolia and Longipetiolata are present, and still mainly through F. brevipetiolata. Fagus brevipetiolata has short, eglandular hairs on the interveinal area of lower leaf-surface. This sort of trichome is found only in F. grandifolia subsp. caroliniana and all of the four species of the section Longipetiolata (F. longipetiolata, F. brevipetiolata, F. tientaiensis, and F. bijiensis). F. grandifolia is characterized by its very short petiole, both in absolute length and relative to the length of the leaf-blade. Such a short petiole is elsewhere only observed in F. brevipetiolata, as correctly expressed by its specific epithet.

Fifth (and finally), the basic leaf-shape of the ancestral populations of F. grandifolia is most probably ovate/elliptic, based on

items 1, 2, and 3. Such a leaf-shape is definitely similar to the ancestral leaf-shape I have previously proposed for the sections Longipetiolata and Lucida, but very different from that of the section Fagus (obovate to obovate/oblong). Along with the conclusion of item 4, it may be concluded that the section Grandifolia is clearly more closely related to the two East Asian sections than to the W Eurasian section Fagus, based on the gross morphology of leaves.

The narrowly triangular cupule-valves of subsp. grandifolia and subsp. mexicana are similar to those of F. engleriana in shape. Considering this trait to be specialized within the genus (and within the two subgenera respectively) is far more convincing than is the opposite supposition. The cupules of subsp. grandifolia and subsp. mexicana are generally slightly larger than those most commonly seen in subsp. caroliniana. Under this situation, the often exserted nuts of subsp. grandifolia may be regarded as caused by an evolutionary enlargement (of the nuts). The long-linear and spreading cupule-appendages of subsp. grandifolia are only occasionally observed in other beech taxa, in which the long-linear appendages, when present, are normally recurved. Those of F. longipetiolata are even often sigmoid. The subulate to short-linear cupule-appendages of the typical white beech are sometimes arranged in clear horizontal rows. Thus, subsp. grandifolia seems to possess four distinct and derived traits of the cupule/nut complex, relative to subsp. caroliniana. Inter-subspecific differentiation in features of cupule/nut complex to such an extent is not found elsewhere within the genus.

After the foregoing comparisons on the overall similarity and

difference in the features of leaf and cupule/nut complex between each of the three subspecies-pairs, it may be perceived that subsp. grandifolia and subsp. mexicana are closer to each other than either of them is to subsp. caroliniana. This point has been mentioned previously, but it looks more clear at this moment. The shape of the cupule-valves and the presence or absence of the short, eglandular hairs on the lower leaf-surface are particularly pertinent to this perception. The former feature has only been used once in the taxonomy of beeches at subspecific level (in F. japonica); whereas the latter has never been applied. Here, the narrowly triangular cupule-valves of the typical gray beech and the Mexican beech can be considered to have developed through parallelism. However, the absence of the short, eglandular hairs in these two subspecies of the American beech is in itself hard to judge to be plesiomorphic or apomorphic within the species. If it is a plesiomorphy, then some evolutionary inferences important both within the species and between sections could be drawn. If it is an apomorphy, then the stunning resemblance between the leaves of F. brevipetiolata and F. grandifolia subsp. mexicana would be sufficiently powerful to allow another version of the evolutionary relationship between the sections Grandifolia and Longipetiolata. Reliable fruiting material of F. brevipetiolata may also offer such a possibility.

The American beech has some other very interesting traits that are not found in, or simply different from those of, any other beech species. The first one is its very broad nuts that almost always have three ridges (= three elevated vascular bundles of the nut-wall) on each side, and are almost constantly rather evenly winged from the top to the

very base. All of these three traits of nuts are absent elsewhere within the genus.

The second is its rarely occurring spathulate-foliaceous, drying greenish/yellowish, multi-veined basalmost cupule-appendages. Non-scale-like, non-subulate, or non-linear cupule-appendages are found elsewhere in F. okamotoi, F. engleriana, F. crenata, and F. sylvatica. In F. okamotoi, the specialized appendages are very-long triangular to nearly strap-like, thin, drying purplish/brownish, and inconspicuously veined. Those of F. engleriana vary from a shape somewhat like the leaves of Potamogeton or Aponogeton to spathulate, thick, drying greenish/yellowish, single-veined to multi-veined. Subspecies hohenackeriana and subsp. sylvatica of F. sylvatica have their lower appendages similar to those of F. okamotoi. Fagus sylvatica subsp. orientalis has its lower appendages conspicuously spathulate, thick, drying greenish/yellowish, and multi-veined. Such a morphology also characterizes the basalmost or lower appendages of F. crenata. However, this sort of appendage only occurs in occasional populations of all of the three subspecies of F. grandifolia, so far as I know. In a few cases the sort characterizing F. okamotoi is also found in F. grandifolia. The characteristic shape of the spathulate appendages of the American beech is well observable in anthesis, but they are mostly caducous before reaching the full length. In the case of the typical white beech, it is bizarre to see a few persistent prominently spathulate appendages on the very base of the cupule, almost immediately above a few persistent bracts of the peduncle (= infructescence axis).

The third is its almost constantly short petiole. As mentioned

before, the leaves of F. brevipetiolata also have a very short petiole. This trait is invariably present in every individual of F. grandifolia examined by me. The only cases in which longer petioles are found are some fertile collections of the Mexican beech. This observation may be taken as a solid evidence supporting an idea that the expression of various gross leaf features on fertile shoots is more specialized relative to that observable on sterile shoots. This supposition is doubtlessly true for the Mexican beech, because the leaves on fertile shoots of this subspecies are mostly trullate or close to trullate, that is definitely more specialized than the lanceolate leaves on sterile shoots. This idea seems to hold true in leaves of many fagaceous taxa, in addition to those of Fagus. It is necessary to clarify in this connection that the morphological difference between sun and shade leaves is not considered here.

The fourth one is the very numerous lateral veins of its leaves. The average number of the secondaries of F. grandifolia is apparently higher than that of any other living taxon of the subgenus Fagus. Moreover, this plesiomorphy (of the subgenus and the genus) is maintained in nearly every individual of this species.

The fifth (and final) one is its serrate leaf-margin. The average serration level of the leaves of the typical gray beech is the highest among all of the beech taxa recognized in this monograph. This level is approached only by some populations of F. sylvatica subsp. hohenackeriana, and occasional populations of F. longipetiolata. As a whole, the species F. grandifolia can be characterized as having serrate leaf-margin. No other beech (sub)species can be so characterized,

except F. sylvatica subsp. hohenackeriana.

To close the discussion of the section *Grandifolia*, I here append some final comments. This section, as represented by a single species, has more numerous stable and nearly unique traits than the other monotypic section, *Fagus*. Most of these interesting traits are not found in the other three sections of the subgenus *Fagus*. Although not all of them are plesiomorphic within the subgenus, they may collectively suggest an isolated taxonomic position for the section *Grandifolia* within the subgenus *Fagus*. In spite of this fact, a close relationship between the section *Grandifolia* and the section *Longipetiolata* can be perceived.

CHAPTER 4

CONCLUSIONS ON EVOLUTION AND PHYLOGENY

In the genus Fagus, features of the structurally simple flowers and inflorescences are either monotonously uniform within the genus or highly variable within individual species. As a result, the primary infrageneric subdivision must rely only on features of the cupule/nut complex and vegetative organs.

With regard to cupules, the following two traits are very evident and have long been regarded as significant in taxonomic and evolutionary considerations: the spathulate-foliaceous cupule-appendages, and the very long cupule-peduncle. The conspicuous and constant presence of spathulate-foliaceous cupule-appendages in F. engleriana (in E Asia) and F. sylvatica subsp. orientalis (in the general region surrounding the Black Sea) serves as one of the few good diagnostic traits differentiating the former from F. japonica (in Japan) and the latter from F. sylvatica subsp. sylvatica (in W Europe). Fagus crenata exhibits a tremendous range in the appearance of its basally-borne cupule-appendages. Some individuals have no spathulate-foliaceous cupule-appendages at all, whereas some others have their cupules highly similar to the typical cupules of F. sylvatica subsp. orientalis. A little known fact is that each of the three subspecies of F. grandifolia has a small proportion of individuals (populations ?) showing several (to many) basally-borne broadly linear to even prominently spathulate-

foliaceous cupule-appendages.

Apically markedly forked spathulate-foliaceous cupule-appendages are found in many individuals of F. engleriana, and a few individuals of F. sylvatica subsp. orientalis and F. grandifolia. They are of normal occurrence in a fossil fagoideae genus Pseudofagus idahoensis of the North American Miocene (Smiley & Huggins, 1981).

Spathulate-foliaceous cupule-appendages are not found in any member of any other fagaceous genus, living or extinct. At the familial level, scale-like appendages should represent the most primitive existing morpho-form in any consideration. They characterize F. lucida and F. japonica subsp. japonica at the present time.

It is self-evident that the spathulate-foliaceous appendages are gross-morphologically connected with the (thin) thread-like and sometimes long-hairy appendages such as those found in F. longipetiolata, F. crenata, and F. sylvatica subsp. sylvatica, and so forth. In turn, a similar connection is also present between the thread-like appendages and the scale-like ones. On the basis of my observations on specimens, at least four different "inter-specific" or "inter-subspecific" transformation series originating from scale-like appendages to thread-like or even to spathulate-foliaceous ones seem to be clearly present.

The first series is supposed to have occurred during the speciation of F. engleriana from a F. japonica-like ancestor. These two species are highly similar in nearly every observable gross-morphological feature, except those of cupule and nuts, and to a lesser extent, bark of the trunk. Their leaves of sterile shoots are often

indistinguishable. Furthermore, all these similarities are exclusive within the genus, except to a lesser extent for F. okamotoi. The cupule-appendages typical for F. japonica subsp. japonica are scale-like, thin, triangular, with a blunt apex, and appressed to, or forming a very small angle with, the surface of cupule-valves. Some of them are slightly thickened at the base. Those typical for F. japonica subsp. angustifolia may also be described as scale-like, but they are (very) long-triangular, thickened in lower portion, then tapering upward to form a glabrous and sometimes short thread-like upper portion. At least the upper portion of these appendages is not appressed on the surface of cupule-valves. The cupule-appendages of F. engleriana may be roughly categorized as being of two kinds. The first is shortly thread-like, prevalent on the upper portion of cupule-valves. The second differs from the first in having a (long)-elliptic or (long)-oblong, greenish, and foliaceous upper portion or tip. In few cases such a foliaceous portion extends downwards to form an oblongate, or even strap-like appendage borne at the very base of cupule-valves. In F. engleriana, the middle portion of the surface of cupule-valves is typically fluted due to the fusion of the basal portion of the appendages with the cupule-wall.

The second transformation series is supposed to have occurred during the speciation of F. okamotoi from a F. japonica subsp. japonica-like ancestor. The information about gross-morphological features of F. okamotoi is incomplete at this moment. Nevertheless, it is very clear that this species belongs to a group which also embraces F. japonica and F. engleriana. The cupule-appendages of F. okamotoi are

long-triangular to shortly linear, nearly membranous, glabrous, and appressed on the surface of cupule-valves.

The third transformation series is supposed to have occurred during the speciation of F. chienii from a pre-F. lucida ancestor and that of F. hayatae from a F. chienii-like ancestor. These three Chinese species are consimilar in gross morphology of leaves, but they differ in the cupule/nut complex. The leaves of the single collection of F. chienii are different from those typical for F. lucida in a few trivial traits. The leaves of F. hayatae may sometimes find counterparts in F. lucida. The cupule-appendages of F. lucida are scale-like, triangular to oblong, with an acute apex, stout, elliptic in cross-section, very hairy, and appressed to, or even with their lower portion coalesced with, the surface of cupule-valves. Some of them have a stout lower portion, abruptly constricted into a free but still appressed shortly subulate and glabrous apex. In F. chienii, the appendages are shortly stick-like, stout, clearly recurved, with their lower portion coalesced with, then conspicuously elevated from, the surface of cupule-valves. The cupule of F. hayatae looks like a miniature of that of F. chienii but beset with proportionally longer and more slender appendages. Sometimes the longer appendages are even slightly sigmoid recurved.

The fourth transformation series is supposed to have occurred during the evolution of the spatulate-foliaceous basal cupule-appendages of F. sylvatica subsp. orientalis from the sometimes-present linear basal cupule-appendages of F. sylvatica subsp. hohenackeriana. Within F. sylvatica, the linear basal cupule-appendages of subsp. hohenackeriana are in turn, derivatives of the thin thread-like

appendages that cover the whole cupule-surface of subsp. sylvatica. All appendages on the whole cupule-surface of the vast majority of the common European beech growing in extra-Mediterranean-Sea W Europe are thin, thread-like, and long-hairy. Some individuals (populations) of the common European beech distributed in Spain, Italy, and C Greece have their basally-borne cupule-appendages very narrowly linear (barely discernible under naked eyes), membranous, and drying-reddish/brownish. This morphological trend is more fully realized in the populations growing in SE Balkans (E Greece, Bulgaria, and S Romania). The subspecies hohenackeriana shows a range of variation in the appearance of basally-borne cupule-appendages throughout its geographic range, but I cannot detect a geographic or ecological covariation pattern in this respect. Some examined individuals have all the appendages on the cupule-surface thin thread-like and very hairy, whereas some others have their basal cupule-appendages linear and varying from membranous and drying reddish/brownish to chartaceous and drying greenish. The basal cupule-appendages of subsp. orientalis are normally foliaceous and drying greenish. They vary considerably in both shape and size. They are more often oblanceolate, sessile, and multi-veined, but they sometimes assume an outline of the leaves of a Potamogeton or an Aponogeton. Their size varies from about 2/5 to about 4/5 as long as the cupule-valves on which they are borne.

Fagus japonica, F. engleriana, and F. okamotoi are collectively characterized by the constant presence of a very long, very slender, and glabrous cupule-peduncle. Regardless of whatever morphological interpretation on the nature of the cupule of the genus Fagus is

adopted, its cupule-peduncle clearly represents a developmentally much reduced inflorescence-axis. Within the genus, a supposedly most primitive, very short, very stout, and very hairy cupule-peduncle is still found in some F. lucida, and in some F. hayatae subsp. hayatae if its cupule and subtending peduncle were enlarged in the same proportion to a certain extent. A very long, very slender, and glabrous infructescence-axis is best regarded as representing a good synapomorphy for an infrageneric group composed of these three E Asian species. The vast majority of plants of F. longipetiolata also have a rather long cupule-peduncle, as do some F. grandifolia subsp. mexicana, some F. sylvatica subsp. hohenackeriana and an even smaller proportion of F. sylvatica subsp. orientalis. Compared with the F. japonica-group, all of these peduncles are stouter, (much) more hairy, and at least when compared with F. japonica and F. okamotoi, definitely shorter in proportion to the length of the cupules atop them. All other beech taxa have much shorter cupule-peduncles than does the F. japonica-group, at least in absolute length, and in most cases also in the relative length to their cupules. Moreover, all of these latest-mentioned peduncles are hairy and (at least proportionally) stouter.

The leaves of the F. japonica-group are invariably very thin (except F. okamotoi whose leaves are just very slightly thicker), constantly with prominently mesh-like epicuticular wax on the glaucous abaxial surface, constantly lacking (clearly defined) primary/secondary pocket-domatia, constantly with very regularly and densely aligned tertiary veins, constantly with a poorly developed higher-order venation pattern, with leaf-margin ordinarily varying from prominently and

smoothly crenate to very slightly undulate. This group is further characterized by very slender (at least when the generally large dimension of its leaves are considered) and glabrous shoots, very prominently stipitate and very slender fusiform buds, low-branching and multi-trunk habit, as well as very large, conspicuous, sometimes even rhombic-shaped fissured old lenticels on trunk-bark. Most of the above-mentioned characteristics are not found elsewhere in the genus. Among these automorphies, some are autoplesiomorphies whereas the others are autapomorphies, for this species group. As a conclusion, it is clear that the F. japonica-group represents an early off-shoot budding out during the early evolutionary history of the genus Fagus. This group was established as a subgenus in Chapter 3: subgenus Engleriana. All other species were then grouped into the other subgenus: subgenus Fagus, which is (almost inevitably) more loosely organized.

Within the subgenus Engleriana, F. japonica subsp. japonica seems to have retained all of the plesiomorphies for the subgenus. Fagus japonica subsp. angustifolia is specialized in its leaf-shape, shape and size of its cupule-valves, and morphology of its cupule-appendages, and it has developed very small triangular extensions along its upper nut-angles. Fagus engleriana appears to have maintained the supposedly most primitive leaf character-states of the subgenus, but has modified the overall features of its cupule and nuts along the way launched by F. japonica subsp. angustifolia. Fagus okamotoi has slightly changed the shape, size, and thickness of its leaves, significantly modified the morphology of its cupule-appendages in another direction, reduced its nut-size, and developed prominent wing-like extensions along its entire

nut-angles.

Within the subgenus *Fagus*, *F. lucida* is the only species that has maintained primitive scale-like cupule-appendages. It also has plump and wingless nuts. Such nuts are only found in *F. japonica* (subsp. *japonica*) elsewhere in the whole genus, and clearly represent a retention of a plesiomorphy of the family. As has discussed previously, *F. lucida*, *F. chienii*, and *F. hayatae* are taxonomically closely related. In addition to a few trivial differences in leaves, *F. chienii* further differs from *F. lucida* in its sometimes slightly winged nuts. *Fagus lucida* shows a clear trend in reducing the number of its cupule-valves to three through lateral fusion of the two valves flanking the two exposed sides of one nut. Once this fusion process is accomplished to produce a very broad and complete cupule-valve, the flanked nut disappears. Such a 3-valved/1-nutted configuration is extremely rarely found elsewhere within the genus as a sort of abnormality, but it is normal and common for *F. lucida*. Many sterile, and even a few fruiting, collections of *F. hayatae* subsp. *pashanica* have been misidentified as *F. lucida*. Some seemingly trivial differences in leaves collectively prove to be taxonomically significant and pertinent in identifying sterile collections of these two taxa. In terms of features of cupule and nuts, however, *F. lucida* and *F. hayatae* are completely different. The cupule/nut complex of *F. hayatae* is invariably very small, and as a unit is definitely only secondary to that of *F. okamotoi* in smallness in the entire genus. [However, in *F. japonica* subsp. *japonica* the definitely smallest beech cupules are also found.] Its thick, thread-like (to subulate), hairy, and often recurved (when long enough) appendages are

similar to those of F. chienii, as mentioned before. Its constantly prominently winged nuts are clearly specialized, probably along with the reduction in size of the cupule. In F. hayatae subsp. pashanica, the cupule-peduncle has been evolutionarily elongated, whereas leaf-size seems to have not been significantly altered. On the contrary, the length of the cupule-peduncle (relative to its cupule) of F. hayatae subsp. hayatae does not appear to be significantly different from that of F. lucida, but the leaf-size of this local subspecies has been reduced to become the smallest one among all living, and most probably also extinct, beech taxa. Only some F. crenata subsp. undulata and some F. hayatae subsp. pashanica (and some of the Japanese Pliocene-Pleistocene fossil populations identified as F. microcarpa) have leaves as small as those of many F. hayatae subsp. hayatae.

Although confined to Japan, F. crenata exhibits tremendous ranges of variation in features of both leaf and cupule/nut complex. Many individuals have leaves without discernible teeth, whereas there are some individuals bearing leaves with discernible, though not sharp, teeth. Many individuals have leaves showing prominently crenate but sometimes centrally depressed intersecondary margin-sections, whereas there are some individuals bearing leaves with rather smooth and straight intersecondary margin-sections. Nevertheless, nearly entire-margined leaves are very rare, and there are no leaves approaching those of F. lucida in leaf-margin configuration. In F. crenata, the following two extremes of cupules are present: the one without foliaceous appendages but almost always with some narrowly linear basal appendages, and the other one with many spatulate-foliaceous basal appendages. The

former looks like a normal cupule of F. longipetiolata when there are no basal linear appendages, whereas the latter is very similar to a normal cupule of F. sylvatica subsp. orientalis. It is important to note here that in no case was a clearly fluted cupule-surface observed in F. crenata. In terms of the morphology of nuts, however, the variation range is narrower. In F. crenata, there is no nut as plump and wingless as the nuts of F. lucida and F. japonica subsp. japonica; at the other end, only a few northern or high-altitudinal individuals (populations) produce nuts as prominently winged as the nuts of F. hayatae.

Again, leaves offer more numerous clues in locating the phylogenetic position of F. crenata within the subgenus *Fagus*. Simply broadening the various variation patterns and trends present in the quartet played by F. lucida, F. chienii, F. hayatae subsp. pashanica, and F. hayatae subsp. hayatae, it appears apparent that F. crenata is well at home within such an enlarged group. The leaves of the common Japanese beech are characterized by their mostly (broadly) rhombic to (broadly) trullate shape, compared with the leaves of the previously-mentioned companions of this species. In other words, they tend to maintain an angle along each side at the broadest portion - here the broadest point, rather than simply exhibiting a smooth curve, in terms of the overall leaf-shape. Angled shapes are clearly specialized in the genus. The expression of all other gross-features and micro-features of leaves are compatible with such a phylogenetic interpretation.

Two subgroups were detected within the concept of F. crenata. The quantitatively major and generally larger-leaved subgroup extends as continuous pure to nearly pure stands in the lowlands of the northern

"Inner Side of Japan" in Honshu. Its populations extend northwards to the lowlands of the southernmost Hokkaido, and eastwards to the mountainous region of N Honsu. In C Honshu, they climb up to about 2,000 m alt. In S Honshu, Shikoku, and Kyushu, the quantitatively minor and generally smaller-leaved subgroup prevails. It is morphologically further characterized by the persistent stipules, the normally nearly wingless nuts, and the often undulate leaf-margin. Its populations flourish within an altitudinal range from ca. 1,000 m to ca. 1,500 m, in a territory south of that of the major subgroup. The northern subgroup is nomenclaturally typical. The southern subgroup was established in the Chapter 3 as the other subspecies: undulata - an epithet long ignored.

The foregoing discussions make me feel comfortable to establish a section (Lucida) to accommodate the perceived phylogenetic relationships among these four species. Three series - Lucidae, Hayatae, and Crenatae - were established to reflect the various degrees of similarities and differences among the species.

The common Chinese beech, F. longipetiolata, has a very long leaf-petiole (both in absolute length and in relative length to the blade), as well as a long cupule-peduncle. Its cupule-appendages are all (thin) thread-like, rather long, often (sigmoid) recurved, and often very hairy. In only a few cases traces of fusion of the basal portion of appendages with the surface of cupule-valves are clearly discernible. In no case is a trend of modification of basally-borne appendages to linear detected. Sometimes those basalmost appendages are clearly shorter than those situated on the middle portion of cupule-valves, well

comparable to the case normal for other fagaceous genera. Its generally rather large leaves are glaucous and whitish tomentose on abaxial surface. This glaucosity is due to the uneven deflection of incident light by the highly papillate epidermis covered with a thick cuticle.

Three other Chinese species were found taxonomically associated with F. longipetiolata: F. bijiensis, F. tientaiensis, and F. brevipetiolata. Once again, vegetative features exert their greatest power here. These four species have their leaves with a lower surface (at least somewhat) glaucous and beset with both glandular hairs (except in F. brevipetiolata) and short eglandular hairs. Similar glandular hairs are found on the leaves of all beech taxa recognized in the present work, except in F. brevipetiolata. The difference in quantity sometimes has some taxonomic significance at the subspecific level. Short eglandular hairs of similar kind are present only on the lower leaf-surface of F. grandifolia elsewhere within the whole genus. The papillate-glaucosity is, however, restricted to the present species-group.

Under SEM, the lower leaf-surfaces of all these four species are consimilar. Stomates are elevated and crowded with many dome-shaped papillae. The latter are generally slightly higher but smaller than the former. Earlier in the growing season mesh-like epicuticular wax is present. The nature of glaucosity of these young leaves is at least in part similar to that of the species of the subgenus *Engleriana*. Such a wax layer is soon converted into a thick continuous plate in older leaves. It is very easy to tell the SEM pictures of species of this species-group from those of any other beech taxa.

The single collection of F. bijiensis has slightly fluted cupules with short awl-shaped appendages and a peduncle much shorter than that of a typical F. longipetiolata. The cupule/nut complex plus its peduncle of the type-tree (two collections available) of F. tientaiensis looks like that of a typical F. hayatae subsp. pashanica except in the following three respects: the cupule is slightly larger, the nuts are less exserted from its subtending cupule-valves, and the wing along the nut-angles is slightly more poorly developed, in F. tientaiensis. This species is further characterized by its thin, elliptic to oblong to ovate, and medium-sized leaves with crenate intersecondary margin-sections connected by small but clear and sharp teeth. In total, F. tientaiensis looks like an intermediate between F. longipetiolata and F. hayatae in many gross features. Nevertheless, the micro-morphology of the lower leaf-surface of F. tientaiensis eloquently supports its taxonomic and phylogenetic position within the subgenus *Fagus*. Some of the Japanese late Upper Miocene-Pliocene fossil populations identified as F. stuxbergii are probably to be associated with F. tientaiensis.

No biologically attached or unabraded detached cupules of F. brevipetiolata are available to me. Within this species-group as characterized before, this species is unique in its very slender and sharply pointed buds, and its lanceolate and very short-petioled leaves with caudate apex and broadly rounded base but without glandular hairs on the lower surface. Such a leaf would be found only on sterile shoots of F. grandifolia subsp. mexicana elsewhere within the entire genus, if the Mexican beech did not have glandular hairs on its lower leaf-surface. Once again, the micro-morphology of the lower surface of

leaves tells us that F. brevipetiolata belongs to the species-group currently discussed. In the present work, a section was established for this micro-morphologically well defined species-group: Longipetiolata.

The great usefulness of the evolution of leaf-margin in circumscribing species-groups of beech may now be discussed. It is clear that there is no good reason to argue against the primitiveness of a serrate leaf-margin within Fagus, when the evolutionary situation of serrate leaf-margin in all other fagaceous genera is considered. In subgenus Engleriana, serrate-margined leaves only sometimes occur on sterile shoots and often prevail on stump-sprouts. On fertile shoots, leaves vary from prominently crenate to nearly entire along the whole margin. Fagus bijiensis is supposed to have retained the most primitive cupule morphology of the section Longipetiolata. Its leaves are serrate to compound-serrate. Compound-serrate leaves are also found in some F. hayatae subsp. pashanica and a few F. longipetiolata. It is self-evident that a compound-serrate margin cannot occur in a leaf with crenate intersecondary margin-sections that is typical for F. tientaiensis, F. chienii, and all F. lucida, normal for many F. hayatae and many F. crenata, and present in a few F. longipetiolata. All the referred-to populations of these six above-mentioned species have clearly discernible small triangular teeth connecting their crenate intersecondary margin-sections, except in some of the referred-to populations of F. crenata and few F. longipetiolata in which the whole leaf-margin is simply crenate. Straight to only very slightly sinuous intersecondary margin-sections are common in F. hayatae and F. longipetiolata.

The foregoing facts unambiguously support an evolutionary transformation series of leaf-margin as follows: beginning with serrate, to straight-slightly sinuous intersecondary margin-sections connected by small triangular teeth, to smoothly crenate intersecondary margin-sections still connected by small triangular teeth. In F. lucida, the teeth are narrowly triangular, always with a very sharp tip, and sometimes even slightly upcurved. Moreover, many specimens of F. lucida have very prominently crenate intersecondary margin-sections. Both traits are apparently uniquely specialized. As mentioned previously, F. crenata has a very broad range in leaf-margin configuration. Within the subgenus *Fagus*, the following three leaf-margin configurations of F. crenata are not found in any other previously-discussed species: nearly entire, a complete leaf-margin composed only of very prominently crenate margin-sections, and a complete leaf-margin composed only of prominently undulate/sinuous margin-sections. All these three should be considered to be specialized following the foregoing comments. Scrupulous observations on various associated intermediate collections further indicate the following fact: the bilaterally uneven development of the teeth had caused a shortened apical teeth-side in some leaves, and had finally resulted in a phenomenal "merging" of the teeth into the intersecondary margin-sections in other leaves.

In this connection, it is notable that a Japanese fossil beech assemblage elegantly suggests several significant evolutionary events. Huzioka & Uemura (1973) published pictures of eight well preserved leaf impressions and two cupule impressions (?) of F. palaeocrenata Okutsu (1955) from a single fossil locality (Hinokinaimatazawa) in Akita

Prefecture of the northernmost Honshu. The fossil flora (Miyata flora) is preserved within the Miyata Formation, and is of late Upper Miocene age (ca. 8-4 my BP, see Uemura, 1988). Of the 2,290 specimens collected from the uppermost member of the Miyata Formation at this locality, 1,867 (incl. leaves, cupules, and nuts) were identified as F. palaeocrenata. Of the eight photographed leaves, one (Pl. 7, Fig. 1) has exclusively typical lower leaf-margin configuration and normal shape and size of sterile leaves of F. hayatae subsp. pashanica (particularly those large-leaved populations). The only arguable point is that its teeth are a bit too large for living F. hayatae. Nevertheless, if such a leaf were representative of a living-plant collection from anywhere around the world, I would assign it to F. hayatae subsp. pashanica without great hesitation. Another leaf (Pl. 9, Fig. 6) is not very clear in its lower margin, it is nevertheless very similar to the previous one. The third leaf (Pl. 9, Fig. 7) can be considered to be a basal leaf on a shoot of an individual of a population which also produced the previous two leaves, based on my experience with living beech species. As to the remaining five leaves, I cannot tell them apart from those produced by some very common living populations of F. crenata. One of them is a terminal leaf (Pl. 7, Fig. 2, the lower one). The two photographed cupules are indistinguishable from slightly abraded cupules produced by living F. hayatae subsp. hayatae. In their supplementary description of cupules of F. palaeocrenata, Huzioka & Uemura (1973: 709) wrote: "...; peduncle stout and short, 1.5 mm thick, 2-5 mm long."

It is very clear to me that the earlier-mentioned three leaves

and the two cupules collectively represent an extinct ancestral population of F. hayatae, bearing leaves very close to those typical for living subsp. pashanica and cupule-peduncles typical for living subsp. hayatae. Okutsu's F. palaeocrenata is a leaf-species. His five photographed leaves (Okutsu, 1955) are indistinguishable from the living F. hayatae subsp. pashanica. His original description and discussions are closely compatible with my concept on such an ancestral F. hayatae. The geological age of Okutsu's plants is similar to Huzioka & Uemura's: Sendai Prefecture of N Honshu, Shirasawa Formation, late Upper Miocene (see also Uemura, 1988). Among the leaves from the entire Miyata flora (five localities) they assigned to F. palaeocrenata (ca. 2,500 specimens), Huzioka & Uemura wrote that "the elliptic leaves with somewhat cuneate base and serrate margin are most dominant ..." With these words, they apparently referred to the nomenclaturally typical F. palaeocrenata, according to my perception as presented above. It seems that cupules compatible with the concept of F. crenata appeared very late in geological history in Japan, probably no earlier than the Pliocene. I do not find a proper name to accommodate the Japanese Upper Miocene fossil leaves very similar to those of living F. crenata but apparently not associated with cupules assignable to F. crenata. For convenience, however, I use the still unpublished name F. uemurae for them.

Tanai correctly transferred Nathorst's Pliocene leaf-species Quercus stuxbergii into Fagus in 1976. He (Tanai, 1976: Pl. 1, Fig. 8) published the picture of his lectotype of this new combination together with another three leaves from the nomenclaturally typical locality:

JAPAN-Kyushu-Nagasaki-Mogi. I cannot distinguish the well preserved lectotype and another two paratypes (Pl. 1, Fig. 4 & 5) from some biologically typical leaves of living F. hayatae subsp. hayatae. However, the remaining one (Pl. 1, Fig. 10; one of Tanai's two hypotypes, the other is Fig. 4) cannot have any counterpart in living F. hayatae subsp. hayatae, F. hayatae subsp. pashanica, or extinct F. palaeocrenata, based on my knowledge. This leaf, another two Tanai's leaves from the same locality (Tanai, 1974: Pl. 4, Fig. 2; Pl. 5, Fig. 5), and many of Nathorst's drawings of Quercus stuxbergii are very similar to those of living F. longipetiolata. The proper name for this sort E Asian Neogene fossil beech leaves is F. protolongipetiolata (Huzioka, 1951: 68-69, Pl. 6, Fig. 3), on the basis of a single leaf impression from N Korean Miocene.

Although this is not an adequate occasion to address further on the neogene fossil history of extant E Asian beeches, some remarks seem to deserve space. The most ancient leaf fossil bearing very close and exclusive similarity to those of the living members of subgenus Engleriana is perhaps the late Lower Miocene (ca. 19 my) leaf photographed by Tanai (Tanai, 1974: Pl. 3, Fig. 2) from Abura of NE Hokkaido. A Middle Miocene beech population from Kavavlja River of C Kamchatka was described as F. evenensis by Chelebaeva in 1980. It is impossible to judge to which living species this leaf-species is biologically closer: F. japonica or F. engleriana, although this sort of NE Asian fossil leaves of Middle Miocene age is generally slightly closer to F. engleriana, in my opinion. Due to the comparatively warmer climate of the Middle Miocene, E Asian beech-containing fossil

assemblages of this age are so far chiefly found in the Far East of Russia. The most ancient fossil cupule bearing great and exclusive similarity to that of living F. japonica (subsp. angustifolia ?) is perhaps the one published by Uemura (1986: Fig. 3; JAPAN-SW Honshu-Okayama-Onbara, Ningyo-toge Formation, late Upper Miocene), along with leaves with a prevailing gross-morphology of living F. japonica (subsp. japonica) (also see Tanai & Onoe, 1961; they established a new leaf-species F. palaeojaponica on the basis of three leaves from Onbara and Ningyo-toge, Ningyo-toge Formation). The most ancient fossil cupules showing great and exclusive resemblance to those of living F. engleriana are probably the two photographed by Huzioka & Uemura (1973: Pl. 8, Fig. 4 & 5; Miyata flora, JAPAN-N Honshu-Akita, ca. 8-4 my), and the one photographed by Uemura (1988: Pl. 2, Fig. 5; Tayama flora, JAPAN-N Honshu-Iwate, ca. 8-4 my). The published leaves associated with these three cupules are better represented in living F. engleriana than in living F. japonica subsp. japonica. It would be reasonable to assign Upper Miocene E Asian fossil leaves of subgenus Engleriana into two taxa.

In Japan, many beech-containing fossil floras with the geological age ranging from Upper Miocene to Pleistocene have been described. The following five statements are likely to be rather close to the facts of geological history. First, at least in N Japan, F. palaeocrenata was predominant in many (early) Upper Miocene forest communities, with F. uemurae and the ancestral populations of F. engleriana being common members of these associations. Second, ancestral populations of F. hayatae subsp. pashanica, F. japonica and F. protolongipetiolata must

have already been in existence during late Upper Miocene in S Japan. Third, F. hayatae subsp. hayatae (= F. stuxbergii Tanai, sensu Shen) and F. crenata (subsp. crenata) must have existed in S Japan during the Pliocene. Ancestral populations of F. protolongipetiolata, F. hayatae subsp. hayatae, and particularly F. hayatae subsp. pashanica are supposed to have dominated many forest communities during the S Japanese Pliocene. Fourth, in Japan, F. crenata and F. japonica gradually became the only two beech species during the Pleistocene, as reflected in fossils. Fagus crenata subsp. crenata became more and more prevalent during later Interglacials in the forested region of the northern "Inner Side of Japan". Fifth, some gross-morphologically distinct leaf-population-groups of F. hayatae and F. crenata had gone extinct in Japan probably prior to the Pleistocene. If they were present nowadays in E Asia, it might be proper to establish additional subspecies to accommodate them.

The foregoing conclusions drawn from fossil materials are generally well compatible with the results of the current interdisciplinary paleoclimatical researches, and the bioclimatical implications of the current geographic and ecological distribution patterns of all of the living E Asian beech taxa.

Now I shall go into the W Eurasian beech taxa. The three subspecies of F. sylvatica have an outstanding unifying characteristic in gross features: constantly prominent wing-like extensions along the whole nut-angles. SEM pictures of the lower surface of their leaves are exclusively consimilar. The differences between their basally borne cupule-appendages have been mentioned before. The higher-borne

appendages are of the same kind in all these three subspecies. They are (thin) thread-like, (densely) long haired, usually (sigmoid) recurved, and sometimes thickened at their attached point with the cupule-surface. In almost no case is a fluted cupule-surface observable. The gross-morphological similarities and differences between their leaves are even more complex and interesting. The leaves on sterile shoots are very characteristic for subsp. hohenackeriana. They would not be mistaken as being produced by any other beech taxa. They are generally (very) large, thin, rhombic to slightly obtrullate, and have 12-15 lateral veins, a prominently serrate upper margin constituted simply by continuous serrations, sharp tooth-tips, an acuminate apex ended by a sharp acme, straight to even slightly incurved tooth-free lower margin ended by a subcordate very-base, and a short petiole. In subsp. orientalis, it is the leaves on fruiting shoots that are diagnostic, particularly for those of NW Anatolian populations. They are medium to small in size, thick, elliptic to obovate, and have 6-10 lateral veins, a slightly serrate to slightly undulate/sinuuous margin, blunt tooth-tips (when present), an acute apex ended by a blunt acme, a narrowly cuneate base, and a long petiole (both in absolute length and in relative length to the leaf-blade). In subsp. sylvatica, there seem to be no significant differences in gross features between leaves on fruiting and sterile shoots. A typical leaf for this subspecies is medium to small in size, thick, (broadly) ovate to (broadly) elliptic/oblong to (broadly) obovate, and has 5-8 lateral veins, a slightly serrate to sinuous to slightly crenate margin (when slightly serrate the teeth are small and blunt-tipped and the intersecondary margin-sections are

slightly sinuous), an acute apex ended by a blunt acme, a cuneate to rounded base, and a long petiole (both in absolute length and in length relative to the leaf-blade).

It is very interesting that the leaves on fruiting shoots of subsp. hohenackeriana are similar to those on sterile shoots of subsp. orientalis. My experience with Fagaceae tells me that when there are appreciable and stable differences between leaves on fruiting and sterile shoots of an adult tree of a taxon, those traits characterizing the leaves on fruiting shoots seem to be more specialized and more rigidly genetically controlled. Thus, subsp. orientalis is likely to be a rather direct derivative of subsp. hohenackeriana, as judged by leaves. This speculation is further supported by their morphology of cupule-appendages, geographic distribution, and their common development of long whitish hairs along major veins on lower leaf-surface, petiole, cupule-peduncle, and current-year shoots.

I see no indications of a direct phylogenetic relationship between subsp. sylvatica and subsp. orientalis. The leaf traits of subsp. sylvatica are mostly specialized ones. This subspecies may be considered to have a sibling relationship with subsp. hohenackeriana. The three-subspecies classification adopted here reflects the anagenetic distance between the Caucasian beech populations and NW Anatolian beech populations. I see no clear and close genetic connections between F. sylvatica and any consubgeneric E Asian taxa. As a result, Fagus sylvatica well deserves a section of its own, in my opinion.

Finally comes F. grandifolia. As in F. sylvatica, the three subspecies recognized here share a common trait: generally well

developed wings along the whole nut-angles. Similarly again, their SEM pictures are collectively readily distinguishable from those of any other beech taxa. Another fact implies a similar genetic potential and/or morphological trend among them: there is a small proportion of populations bearing at least clearly linear basally-borne cupule-appendages in each of the three subspecies. Their cupule-surfaces are always clearly fluted. Their leaves are large, with very numerous lateral veins (to 22 in leaves on sterile shoots), serrate-margined, very short-petioled (on sterile shoots), and with short whitish eglandular hairs on lower surface. They finally share an interesting trait of nut: there are always longitudinal ridges on nut-surfaces. Nevertheless, there are enough differences among these three subspecies in other gross-features of cupules and leaves.

A typical subsp. grandifolia has cupule-valves narrowly triangular and grayish/yellowish tomentose when dry; cupule-appendages thin thread-like, long, spreading outward, densely long-hairy, with the lower portion fused with the cupule-surface; nuts exserted from the cupule-valves; and leaves (on fruiting shoots) rhombic, sharply and coarsely serrate. A typical subsp. caroliniana has cupule-valves ovate and brownish/reddish tomentose when dry; cupule-appendages subulate, stout, short, spreading outward to slightly recurved, with the lower half fused with the cupule-surface then resulting in a very prominently fluted cupule-surface; nuts roughly level with the cupule-valves; and leaves oblong to elliptic, often with a subcordate very-base, with a tomentum on the lower-surface that is made up of short whitish eglandular hairs, and with a slightly serrate margin with to without

rather straight intersecondary margin-sections. A typical subsp. mexicana has cupule-valves narrowly triangular and grayish/yellowish tomentose; cupule-appendages awl-shaped/thread-like, thin, short, spreading outward, with the lower half fused with the cupule-surface; nuts exserting from the cupule-valves; and leaves lanceolate and slightly serrate with to without rather straight intersecondary margin-sections (on sterile shoots) or trullate and serrate (on fruiting shoots).

It is clear to me that there exist three distinctive beech population-groups in the American continent, and that there exist no direct phylogenetic relationships between any pair of them. Nevertheless, it is also clear that the leaves of subsp. mexicana are more specialized, and that the overall traits of the cupule of subsp. caroliniana are more primitive, within the species. Based on my experience with the beeches growing outside the America, it may also be possible that the leaves of subsp. caroliniana have on the average retained more numerous plesiomorphies of F. grandifolia than have the other two subspecies. Finally, the species F. grandifolia apparently merits a section status of its own.

Prior to the end of this chapter, some facts and reasonings associated with the evolution and taxonomy of beeches may be presented. I shall first mention the size and shape of trees, the basic adaptation in temperature and growing-season rainfall, and the vegetation niche, of the taxa recognized in the present work.

Both F. japonica and F. engleriana are low-branching bush-like trees. Naturally, they cannot attain great size. Nevertheless,

individuals 25 m tall are not very rarely seen, and a 70 cm DBH could be attained. Both are mesic trees. Fagus japonica is a MMF-associated species, whereas F. engleriana often forms pure or nearly pure stands in Northern Hardwood belt. The supposed switch of F. engleriana in temperature adaptation well corresponds to its specialized expressions in the overall features of cupule and nuts.

All taxa of subgenus *Fagus* are high-branching trees with a rather straight trunk when growing in forest, but the size they could attain differs from taxon to taxon. Fagus longipetiolata seems very seldom to reach 25 m in height, and a DBH of 50 cm is normal for a fairly tall individual of this species. Fagus hayatae subsp. hayatae is interesting in its overall small dimensions in important gross features. I do not know whether there is an individual as much as 20 m tall on record. A DBH of 50 cm is perhaps similarly rare for this taxon. Fagus lucida, F. hayatae subsp. pashanica, and F. crenata are tall and stout trees. The former two taxa rather commonly reach a height of about 25 m, and a DBH of about 1 m. For F. crenata, at least subsp. crenata, individuals of 30 m x 1.5 m dimension are normally found in old stands on high-quality sites.

Among the four major beech species growing in Mainland China, the geographic range of F. longipetiolata is definitely most southern, despite of the extensive overlappings between taxa. Furthermore, when F. longipetiolata occurs along with other beech(es), it invariably prevails within a lower altitudinal range. Its populations seem to be chiefly found in the transitional belt between a MMF and a subtropical notophyllous forest. It is sometimes present in rather dry habitats, if

the relative humidity is high enough.

Some of the above-mentioned traits of the common Chinese beech are unique for beeches, whereas the remaining are unusual. Some of these traits are very likely plesiomorphic for the subgenus, even for the whole genus, whereas the remaining are clearly specialized ones.

Fagus lucida and F. hayatae subsp. pashanica have similar habitat, similar geographic range, similar tree-size, and similar leaves (the type collection of F. lucida is a mixed collection of these two taxa). In the common northern range of these two taxa in NW Hubei and NE Sichuan, F. engleriana often prevails at higher elevations. In the southern range of F. lucida in Gueizhou where F. hayatae subsp. pashanica does not occur, F. lucida is sometimes found in drier habitats along with F. longipetiolata. It is worthwhile to note in this connection that no hybrids between any two of these four major Chinese beeches have been detected.

The overall ecological adaptations of F. crenata subsp. crenata are comparable with those of F. engleriana. Thus, within section Lucida, we see this taxon has highly specialized leaves, most specialized basally-borne cupule-appendages, largest tree-size, and highest degree of cold-resistance. A quite beautiful combination !

All subspecies of both F. sylvatica and F. grandifolia seem to be more fast-growing than the E Asian beeches, and they can easily reach 40 m tall and a 1.5 m DBH on high-quality sites. Compared with F. lucida and F. crenata (subsp. crenata) of the E Asian section Lucida, trees of the W Eurasian and N American sections are more slender.

Another interesting comparison between the E Asian beeches and

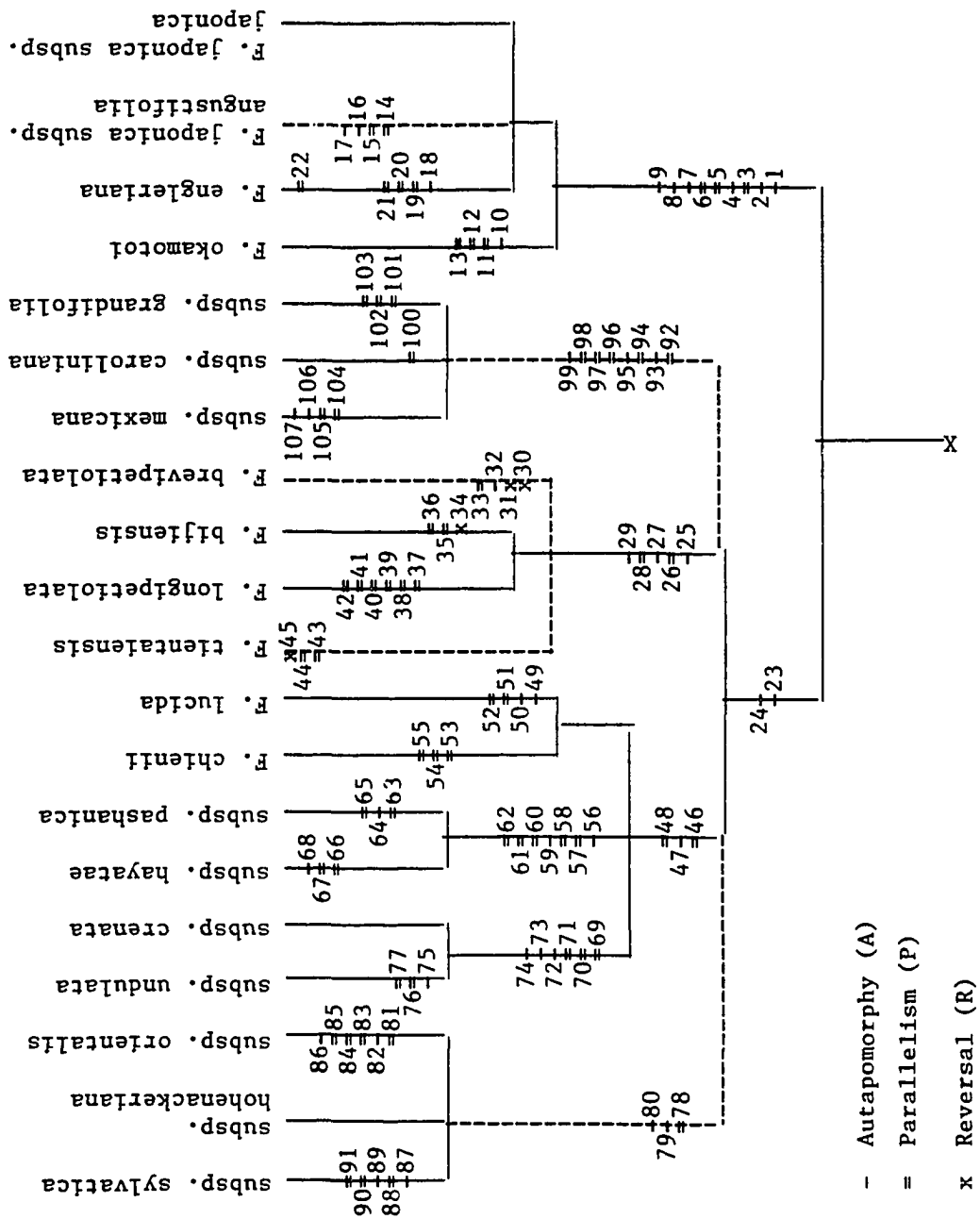
beeches growing outside E Asia is: all E Asian beeches now grow in non-glaciated area, whereas F. sylvatica subsp. sylvatica and F. grandifolia subsp. grandifolia may be said to have the vast majority of their populations in the area that had been covered by the last and strongest advance of continental glacial. These two taxa have reached or almost reached the limit of cold-resistance for a large deciduous hardwood tree. Fagus grandifolia subsp. grandifolia has a very high percentage of hollow-seeds, but has a very strong ability to regenerate by root-sprouts. Fagus sylvatica subsp. sylvatica shows a roughly parallel migration rate and geographic pattern of post-glacial range-shift to those of human activities during the same period in Europe. This implies a "weedy" habit for the common European beech, which in turn may have something to do with the more and more drastically fluctuating climates since the Pliocene during which this taxon is supposed to have taken shape.

The general ecological adaptations of F. grandifolia subsp. caroliniana do not seem to differ significantly from those of F. longipetiolata. This sort of habitat is probably not very dissimilar to the habitat in which the genus Fagus had evolved some of its critical ecological traits such as deciduousness.

There seem to be no significant differences in gross morphology of seedlings among beech taxa. The two eophylls are foliaceous and opposite. Their lateral veins are generally few in number, often not straight, not smooth, and often markedly dichotomously branching in the exmedial half. Their tertiary venation is highly irregular. Their margin is serrate, with the teeth sometimes very blunt-tipped. They are

seemingly products of a loose or not-well-organized genetic control system. The two pairs of interpetiolar stipules are sometimes clearly observable. They are lanceolate, assuming a general appearance not significantly different from the stipules of the adult trees of many other fagaceous genera. Leaves on young root-sprouts are generally similar to the eophylls, except the larger size of the former.

A phylogenetic diagram of the genus Fagus is presented as follows:



EXPLANATION OF NUMBERS IN THE PHYLOGENETIC DIAGRAM:

- 1(A): prolonged, slender, glabrous cupule-peduncle.
2(A): two protuberant scars of the two subtending bracts of female inflorescence, at the distal end of cupule-peduncle.
3(P): wax-glaucosity of lower leaf-surface.
4(A): often bowl-shaped cells on and adjacent to the veins on both leaf-surfaces.
5(P): stomatal complex lacking clearly defined subsidiary cells.
6(P): thin leaves.
7(A): stipitate buds.
8(A): low-branching and thus bush-like tree-shape.
9(A): prominently fissured old lenticels on bark.

Subgenus Engleriana

- 10(A): tiny nuts, level with the cupule-valves.
11(P): prominently winged nuts.
12(P): long-triangular to linear cupule-appendages.
13(P): smaller leaves.

F. okamotoi

- 14(P): very slightly winged nut-apex.
15(P): long-triangular cupule-valves.
16(A): long-triangular, scale-like cupule-appendages.
17(A): narrow leaves.

F. japonica ssp. angustifolia

- 18(A): small, triangular wing at nut-apex.
19(P): long-triangular cupule-valves.

20(P): large cupule.

21(P): thread-like upper cupule-appendages

22(P): constant presence of basal spatulate-foliaceous lower cupule-appendages.

F. engleriana

23(A): clearly defined primary/secondary pocket-domatia.

24(A): well developed venation within vein-islet.

Subgenus Fagus

25(A): broad, blunt buds.

26(P): tomentum made up of short, eglandular hairs on lower leaf-surface

27(A): dome-shape epidermal cells of the lower leaf-surface, and thus papillate-glaucosity on the lower leaf-surface.

28(P): wax-glaucosity on lower leaf-surface of young leaves.

29(A): specialized cells on veins of leaves.

Section Longipetiolata

30(X): lack of glandular hairs on lower leaf-surface.

31(X): slender, acute buds.

32(A): specialized subsidiary cells of the short, eglandular hairs on lower leaf-surface.

33(P): lanceolate leaves.

F. brevipetiolata

34(X): elliptic nuts.

35(P): subulate, short cupule-appendages.

36(P): compound-serrate leaf-margin.

F. bijiensis

37(P): thin, thread-like cupule-appendages.

- 38(P): large cupule.
39(P): long cupule-peduncle.
40(P): long leaf-petiole.
41(P): large leaves.
42(P): often oblong leaves.

F. longipetiolata

- 43(P): prominently winged nuts.
44(P): subulate to thread-like cupule-appendages.
45(X): thin leaves.

F. tientaiensis

- 46(P): at least somewhat crenate intersecondary margin-sections of
leaves.
47(A): often sharp, though small, teeth connecting the intersecondary
margin-sections.
48(P): strongly elevated periclinal walls of epidermal cells of the
lower leaf-surface.

Section Lucida

- 49(A): often 3-valved/1-nutted cupule/nut complex.
50(A): often very sharp, small, narrowly triangular, upcurved teeth on
leaf-margin.
51(P): often prominently crenate intersecondary margin-sections.
52(P): sometimes lanceolate leaves.

F. lucida

- 53(P): subulate cupule-appendages.
54(P): large cupule.
55(P): very slightly winged nut-apex.

F. chienii

- 56(A): small nuts, generally exserting from the cupule-valves.
57(P): prominently winged nuts.
58(P): subulate to thread-like cupule-appendages.
59(A): small cupules.
60(P): not prominently elevated periclinal walls of the epidermal cells
on the lower leaf-surface.
61(P): small guard cells of the stomates.
62(P): the two guard cells of the stomates casting a circular external
outline.

F. hayatae

- 63(P): longer, more slender cupule-peduncle.
64(A): often deeper notch between the basalmost tooth and the basalmost
intersecondary margin-section, than the upper notches.
65(P): often oblong leaves.

F. hayatae ssp. pashanica

- 66(P): smaller leaves.
67(P): often ovate to lanceolate leaves.
68(A): small tree-stature.

F. hayatae ssp. hayatae

- 69(P): the frequently seen basal spatulate-foliaceous cupule-
appendages.
70(P): longer cupule-peduncle.
71(P): larger cupule.
72(A): broadly rhombic to broadly trullate leaves.
73(A): rather commonly seen strongly crenate leaf-margin.

74(A): often sinuous leaf-margin, caused by the "merging" of the teeth
into the intersecondary margin-sections.

F. crenata

75(A): persistent stipules.

76(P): smaller leaves.

77(P): often undulate leaf-margin.

F. crenata ssp. undulata

78(P): prominently winged nuts.

79(A): long-hairy on vegetative organs.

80(A): nearly always detectable linear or linear-like basal cupule-
appendages, when spatulate-foliaceous ones are absent.

Section Fagus

81(P): constant presence of basal spatulate-foliaceous cupule-
appendages.

82(A): often obovate leaves.

83(P): often sinuous/undulate leaf-margin.

84(P): smaller leaves on fruiting shoots.

85(P): long-petioled leaves on fruiting shoots.

86(A): often acute-apexed and blunt-acmed leaves on fruiting shoots.

F. sylvatica ssp. orientalis

87(A): mostly broadly elliptic leaves, sometimes approaching circular.

88(P): smaller leaves.

89(A): few lateral veins.

90(P): often crenate leaf-margin.

91(P): often acute-apexed and blunt-acmed leaves.

F. sylvatica ssp. sylvatica

- 92(P): prominently winged nuts.
- 93(A): prominently striate (=ridged) nut-surface.
- 94(P): tomentum made up of short, eglandular hairs on lower leaf-surface.
- 95(A): sunken veins of higher orders on both leaf-surfaces.
- 96(P): small guard cells of the stomatal complex.
- 97(P): the two guard cells of the stomatal complex casting a circular external outline.
- 98(P): stomatal complex lack of clearly defined subsidiary cells.
- 99(A): very short petiole of leaves on sterile shoots.

Section *Grandifolia*

- 100(P): often oblong leaves.

F. grandifolia ssp. *caroliniana*

- 101(P): long, thin, thread-like cupule-appendages.
- 102(P): narrowly triangular cupule-valves.
- 103(P): often rhombic leaves.

F. grandifolia ssp. *grandifolia*

- 104(P): short, thread-like, sometimes slightly recurved cupule-appendages.
- 105(P): narrowly triangular cupule-valves.
- 106(A): trullate and smaller leaves on fruiting shoots.
- 107(A): lanceolate and larger leaves on sterile shoots.

F. grandifolia ssp. *mexicana*

APPENDIX 1

A CLASSIFICATION SYSTEM OF THE GENUS FAGUS TOURN. EX L.

SUBGENUS ENGLERIANA Camp ex Shen, subgen. nov.

F. engleriana Seemen

F. japonica Maxim. subsp. japonica

subsp. angustifolia Shen, subsp. nov.

F. okamotoi Shen, sp. nov.

SUBGENUS FAGUS

SECTION LONGIPETIOLATA Shen, sect. nov.

F. longipetiolata Seemen

F. brevipetiolata Hu

F. bijiensis C.F. Wei & Y.T. Chang

F. tientaiensis T.N. Liou

SECTION LUCIDA Shen, sect. nov.

SERIES LUCIDAE Shen, ser. nov.

F. lucida Rehder & Wilson

F. chienii Cheng

SERIES HAYATAE Shen, ser. nov.

F. hayatae Palibin subsp. hayatae

subsp. pashanica (C.C. Yang) Shen, comb. nov.

SERIES CRENATAE Shen, ser. nov.

F. crenata Blume subsp. crenata

subsp. undulata (Buerger) Shen, comb. nov.

SECTION FAGUS

F. *sylvatica* L. subsp. *sylvatica*

subsp. *orientalis* (Lipsky) Greuter & Burdet

subsp. *hohenackeriana* (Palibin) Shen, comb. nov.

SECTION GRANDIFOLIA Shen, sect. nov.

F. *grandifolia* Ehrh. subsp. *grandifolia*

subsp. *caroliniana* (Loudon) Camp ex Shen,

comb. nov.

subsp. *mexicana* (Martinez) Camp ex Shen,

comb. nov.

APPENDIX 2

CITATION OF EXAMINED COLLECTIONS

FAGUS ENGLERIANA SEEMEN (CHINA & KOREA) (all collections examined)

CHINA, SHAANXI: Danfeng: SB He 354, IBSC-457078; HANYIN: BZ Guo 2134, CDBI-41794, PE-270950.

CHINA, HENAN: Lushi: Collector unknown, 1959-7-12, PE-34583.

CHINA, SICHUAN: Chengkou: TL Dai 101065, CDBI-41801; TL Dai 105771, CDBI-41811; TL Dai 105971, CDBI-41797; (Emeishan): ZB Peng 6210, PE, IBSC-394955; Guan: WP Fang 2221, NY, E(2); Meigu: Collector unknown 1976-7-30, CDBI-41795; Nanchuan: Acad. Sin. Phytogeogr. 1978 Exp. 644, CDBI-72289; P Bork & A v Rosthorn 1525; Nanjiang: JW Ge, Nanjiang Pop. 1, 1988-10-28, NY; JW Ge Nanjiang Pop. 2, 1988-10-28, NY; Tienquen: FJ Dai 4244, A; Tongjiang: Chongqing Norm. Univ. & Northw. Agr. Univ. 1960 Exp. 42, CDBI-41806; Wanyuen: Chongqing Norm. Univ. & Northw. Agr. Univ. 1960 Exp. 6084, CDBI-41802; Wushan: GH Yang 59045, CDBI-41793; EH Wilson Veitch-747, NY; Wushi: Collector unknown 227, 1960-7-13, CDBI-2180; GH Yang 59234, CDBI-41812; GH Yang 61322, CDBI-41799; GH Yang 65075, CDBI-41798; GH Yang 65410, CDBI-41807.

CHINA, HUBEI: Badong: EH Wilson Veitch-256, A, E, NY, US-596382; EH Wilson Veitch-447, A, E, K, US-596448; Fang: A Henry 6797, E, G, GH; EH Wilson AA-704, A(2), E, GH, US-777128; Jienshi: EH Wilson Veitch-447, A; Shennongjia: Sino-Am W Hubei 1980 Exp. 1221, E, NY; Sino-Am W Hubei 1980

Exp. 1309, A, NY; Xienfeng: HJ Li 58-17, PE-737811; Xingshan: EH Wilson AA-703, A.

CHINA, ZHEJIANG: Anji: SX Huang L-8534-134, ZJFC; Lin'an: CF Shen 1763, NY.

CHINA, ANHUEI: (Huangshan): M Chen 1152, PE; RC Ching 2967, A, E, US-1430575; MP Deng & K Yao 79-207, A; MJ Wang 3839, IBSC-262147.

KOREA, KYONBUK: Ullung (Ulreung-Do): CS Chang 121, NY; CS Chang 136, NY; J Murata et al. 21175, TI; H Ohashi & Y Tateishi 8331, cult., in Nikko Bot. Gard. of Tokyo Univ., in Honshu-Tochigi, TUS-74532; T Nakai 4213, TI; T Nakai 4217, TI; EH Wilson 8497, A(5), E(2), G, US-1092442.

FAGUS JAPONICA MAXIM. SUBSP. JAPONICA (JAPAN) (all collections examined)

HONSHU, IWATE: K Sohma & H Ohashi 134, TI; Miyagi: A Kimura 1943-2-21, TUS-22468, TUS-22474; T Nakamura 1981-5-24, TUS-70370; H Ohashi 2919, TI; K Otomo 1976-4-22, TI-1316788; K Sohma 1364, TI, TUS-37752; K Sohma 3404, TUS-68762; Yonebayashi et al. 1982-4-23, TUS-71911; Fukushima: Y Tateishi & TT Chen 10237, TUS-99724; H Ohashi & Y Ueno 8569, TUS-85228; MAK-50110; Ibaraki: T Nagayama 559, TUS-95882; Collector unknown 1905-0-0), MAK-50108; Tochigi: J Bisset 1199, E; J Bisset 4256, E; H Sakurai 1910-8-21, A; H Sakurai 1911-8-17, E; CS Sargent 1892-0-0, A; EH Wilson 6733, A, GH; Gunma: CS Chang 700, NY; J Murata et al. 2282, A, NCU-470414; MAK-2028; MAK-2029; Tokyo: U Faurie 1797, A, E, G(3); T Makino 1904-4-24, MAK-50115; T Makino 1915-0-0, MAK-50121; T Makino 1926-4-0,

G-20986; T Makino 1926-0-0, MAK-50123; H Takeda 1904-7-6, E; EH Wilson 1904-8-16, A; Herb. Yokohama Nursery Co., Ltd. 1909-4-24, E; Collector unknown 1910-8-16, US-1176242; Kanagawa: Tschonoski 1864-0-0, A, G, GH, US-39343; K Hisauchi 1926-10-3, TUS-22466; Nagano: M Minemura 1961-8-10, MAK-17801; S Noshiro 1646, TUS-75430; Gifu: M Mizushima 1954-8-19, MAK-2030; Shizuoka: Y Kadota 527, TI-1338092; Aichi: K Torii 1947-7-6, TI; Wakayama: H Ohashi 68-610, TI; Shimane: H Mayr 1886-5-12, A; K Shiota 2688, A; MAK-15812.

SHIKOKU, Ehime: MAK-50095; Kochi: N Inagaki 1968-8-9, TI; M Yamanaka 1955-9-26, TUS-50723.

Localities unknown: Collector unknown, L-16907-71; Collector unknown, L-16907-75-A.

FAGUS JAPONICA MAXIM. SUBSP. ANGUSTIFOLIA SHEN (JAPAN) (all collections examined)

Locality unknown: three cultivated trees of different origin in the Arnold Arboretum, Massachusetts, U.S.A.: AA-23182-A, AA-5277-B, and AA-14587-B (not very "pure"?).

FAGUS OKAMOTOI SHEN (JAPAN) (all collections examined)

HONSHU, Tochigi: J Bisset 4256, E, (not very "pure?"); H Hara & H Ohashi 1970-7-23, TUS-63872; CS Sargent 1885-8-0, (materials contained in package excluded), A; CS Sargent 1892-0-0, A, (not very "pure?");

Tokyo: S Suzuki 238, A; **Yamanashi:** S Noshiro 1606, TUS-75454; **Nagano:** S Noshiro 1646, TUS-75430;

FAGUS LONGIPETIOLATA SEEMEN (CHINA & VIETNAM) (all collections examined)

CHINA-SICHUAN: **Chengkou:** RP Farges 1557-A, G; **Hongshi/Lewu:** Sichuan Econ. Pl. Liangz. 1959 Exp. 1495 (= SR Liou & GH Yang 1959-7-30, CDBI-2210; **Leipuo:** Sichuan Econ. Pl. Liangzhou 1959 Exp. 562, CDBI-2184; **Mabien:** FT Wang 23034, A; **Mupin:** EH Wilson Veitch-4499, A; EH Wilson AA-2791, A, E, GH; **Pingshan:** Sichuan Econ. Pl. Ibin 1959 Exp. 1217, PE, CDBI-2190; **Shizhu:** Y Chen 724, CDBI-49961; Y Chen 932, CDBI-49932; **Songpan:** Sichuan Econ. Pl. Aba 1959 Exp. 1716, CDBI-2192; **Tienquen:** Sichuan Econ. Pl. Ya'an 1959 Exp. 738, CDBI-2185; FD Pu 53, CDBI-2183; **Wan:** CT Hua 36, A; CT Hua 321, A; **Wushan:** EH Wilson Veitch-608, A, E, NY, US-596505; EH Wilson AA-460, A, E, GH, US-777053; EH Wilson AA-700, A; **Locality unclear:** southern border of Gansu, FT Wang 22534, A.

CHINA-HUBEI: **Badong:** A Henry 5334, E, G(2), GH, K, US-801056; A Henry 7444, GH, K, US-802090; EH Wilson AA-493, A(2), E(3), G, GH, K, US-777057; EH Wilson AA-700-A, A; **Changyang:** EH Wilson AA-700-B, A, E, GH(2), US-777127; **Jiensi:** A Henry 5334, E, G(2); A Henry 5334-A, A(2), E, G, GH, K, US-598673, US-801057; EH Wilson Veitch-537, E; **Lichuan:** WC Cheng & CT Hua 667, A; JL Gressitt 2481, (not very "pure"?), A; **Xienfeng:** WB Lin 646, PE-743407.

CHINA-HUNAN: **Jianghua:** BG Li & SB Wan 5223, IBSC-436452; **(Mubushan):** YK

Hsiung 5834, A; Sangzhi: BG Li & SB Wan 75-212, PE-1151581; Wugang:
Handel-Mazzetti 2200, A; Handel-Mazzetti 2491-A or 11112 ?, A(2), E, G;
Wuling: L Liou et al. 632, NY; L Liou et al. 1672, NY; Yuenling: L Liou
et al. 335, NY.

CHINA-GUEIZHOU: Dushan: Y Tsiang 6549, NY; Duyun: Y Tsiang 5890, NY;
(Fanjingshan): AN Steward et al. 729, A(2), ECON; Gueiyang: Y Tsiang
8429, E, NY, US-1578676; Nayong: Acad. Sin. Bijie 1959 Exp. 573, PE;
Tongzi: Y Tsiang 5025, A, MU, NY; Yinjiang: Sino-Am Gueiz. 1986 Exp.
1304, NY; Zhenfeng: Y Tsiang 4642, NY.

CHINA-YUNNAN: Gujiau: J Cavalerie 2119, E; J Cavalerie 2279, E; J
Cavalerie 2303, E; Jinping: Sino-USSR Yunnan 1956 Exp. 1530, PE; Mengzi:
A Henry 9027, A, E, K, NY; A Henry 9202, NY; Pingbien: HT Tsai 62769, A;
Wunshan: KM Feng 11276, A; KM Feng 22576, IBSC-386921; Xichou: KM Feng
11543, A; KM Feng 11840, A.

CHINA-GUANGXI: Chuenyuen: TS Tsoong 81938, A; Lucheng (Miaushan): RC
Ching 5944, A, NY; Lingyun: AN Steward & HC Cheo 190, A, G, NY;
Longsheng: HF Qin & ZT Li 70281, IBSC-273256; Tienlin: ZT Li 60-687, PE;
(Yaoshan): C Wang 40543, A; Zhenbien: SP Ko 56047, A.

CHINA-GUANGDONG: Changtungchang: H Fenzel 5845, A; Lechang: CL Tso 20560,
 NY(2); CL Tso 20647, A, NY; Lien: PX Tan 60039, IBSC-284375; Yingde: SP
Ko 50457, PE-506482; Wang & Ling 7348, A; (Yaoshan): SS Sin 9943, NY;
Xinfeng: YW Taam 599, A, E, G-275280, MICH; YW Taam 738, A, G-275318,
 MICH.

CHINA-JIANGXI: Chongyi: MX Nie et al. 8779, IBSC-391846; Hongsan: JL
Gressitt 1444, A, E, G; Qienshan: SS Lai 4241, PE-762658; Xioushuei: YK
Hsiung 6534, A.

CHINA-FUJIE: Changting: QM Hu 3661, IBSC-392076; Jienning: ZY Li 10943, PE-1213669; Shouning: RC Ching 2273, A, K, NY, US-1247115.

CHINA-ZHEJIANG: Taishun: RC Ching 2141, A, E, NY(3), US-1246987; YL Keng 318, A; SY Zhang 5727, PE-699274; Tientai: RC Ching 1451, A(2); RC Ching 1476, A(2); YL Keng 1081, A; Jinyun: CS Ding & LH Lou 914, ZJFC; Kaihua: Li & Zheng 344, ZJFC; Qingyuen: S Chen 3376, A; Sueichang: S Chen 1166, A.

CHINA-ANHUEI: Wuyuen: RC Ching 3216, A, E, US-1430628.

VIETNAM-TONKIN: Chapu: A Petelot 4313, NY, US-1577711; A Petelot 7898, A.

FAGUS BREVIPETIOLATA HU (CHINA) (all collections examined)

SICHUAN, Nanjiang: JW Ge Nanjiang Pop. 2, 1988-10-27, NY.

HUBEI, Badong: EH Wilson AA-493, EH Wilson AA-700-A, EH Wilson AA-700-B, GH; Lichuan: JL Gressitt 2467, A.

GUEIZHOU, Gueiding: Y Tsiang 5457, NY.

YUNNAN, Malipuo: KM Feng 13815, A.

GUANGDONG, (Mahang): WY Chun 5962, A.

Localities unknown: EH Wilson 7000 (?), C Schneider 1916-9-18, cult. in A, US-1523753; Collector unknown 8241, K (Photo in NY).

FAGUS BLIENSIS CF Wei & YT CHANG (CHINA) (all collections examined)

GUEIZHOU, Bijie: PH Yu 766, PE.

FAGUS TIENTAIENSIS T.N.LIOU (CHINA) (all collections examined)

ZHEJIANG, Tientai: S Chen 3718, A; LH Lou 6064, ZJFC.

FAGUS LUCIDA REHDER & WILSON (CHINA) (all collections examined)

SICHUAN, Erbien: CL Chang 64-212-A, IBSC-377772; Chengkou: RP Farges 1557, E, G(3), NY; Shimien: CC Hsieh 42274, PE-538759; Wan: WC Cheng & CT Hwa 1058, A; Yunlien: KL Qiou 80, CDBI-41627.

GUEIZHOU: (Fanjingshan): AN Steward et al. 389, NY; AN Steward et al. 662, NY, US-1598925; Ronjiang: S Gueizhou 1959 Exp. 3191, PE-683320.

HUBEI: Xingshan: EH Wilson AA-715-A, A; EH Wilson AA-715-C, A; EH Wilson AA-715-D, A; EH Wilson AA-715-E, US-777132; Hefeng: HJ Li 6339, PE-737882; Shennongjia: 1980 Sino-Am W Hubei Exp. 1479, A, NY.

HUNAN: Nanyue: Huazhong Agr. Coll. 64-107, ZJFC; BG Li 504, IBSC-230657; Y Liu 245, PE-313618; (Mufushan): YK Hsiung 5886, A; Xinning: CS Fan & YY Li 430, ECON, G.

GUANGXI: Damiaushan: SQ Chen 14533, IBSC-286668; SQ Chen 15504, PE-806241; Lucheng: RC Ching 6272, A, NY.

GUNAGDONG: Lechang: TS Chu 359, IBSC-164558.

FUJIAN: Taining: GL Cai 400, IBSC-447875.

FAGUS CHIENII CHENG (CHINA) (all collections examined)

SICHUAN: Pingwu: WC Cheng 2903, A, E, IBSC-54558, MICH, PE, US-1626932.

FAGUS HAYATAE PALIBIN SUBSP. HAYATAE (CHINA-TAIWAN) (all collections examined)

TAIWAN: Taipei/Taoyuen: PC Chung & LM Chang 1951-5-0, A, TAIF; ZX Xie & QX Xiao 1988-9-7, population sample (20 individuals); Hino 7362, TAI; R Kanehira 1919-10-8, A; R Kanehira & S Sasaki 40, A, TAIF; N Konishi 1906-2-0, TI (Photo); N Konishi 36413, TAI; M Konishi 1918-8-22, A; M Minaki et al. 2110, TI; T Suzuki 4630, TAI; T Suzuki 8658, TAI; T Suzuki 18514, A, MICH, US-2063411; KC Yang 1328, TAI-36407, TUS-79649; SS Ying 4708, TAF; Ilan: T Suzuki 5960, TAI.

FAGUS HAYATAE PALIBIN SUBSP. PASHANICA (C.C. YANG) SHEN (CHINA) (all collections examined)

SICHUAN: Nanjiang: Chongqing Norm. Coll. & Northw. Agr. Coll. 1960 Exp. 3099, CDBI-41631; JW Ge 1988-10-26, Pop. 1; JW Ge 1988-10-27, Pop. 2; CC Yang 75-011, CDBI-41628, FJSI, PE, ZJFC, Sichuan 1 For. Surv. Team (3);
Tongjiang: Chongqing Norm. Coll. & Northw. Agr. Coll. 1960 Exp. 33, CDBI-41630.

HUBEI: Fang: A Henry 6793, IBSC-344388, K, GH, US-801860; Ichang: HB Chen 1988-9-10, FJSI-29221; Shennongjia: 1980 Sino-Am W Hubei Exp. 1485, A, NY; (Suon Nai Ook): WY Chun 4182, A; Xingshan: EH Wilson AA-715-B, A.

HUNAN: (Mufushan): YK Hsiung 5852, A.

ZHEJIANG: Yongjia: MX Wu 619, FJSI-18706, ZJFC; MX Wu 81-149, FJSI-18427, FJSI-18428, ZJFC; MX Wu 1985-0-0, FJSI-25209, ZJFC; MC Liou 84-45, FJSI-24164, FJSI-24165, ZJFC; MC Liou 1985-4-0, FJSI-25214, ZJFC; SL Zhou 433, ZJFC.

FAGUS CRENATA BLUME SUBSP. CRENATA (JAPAN) (selected collections examined)

HOKKAIDO: Maximowicz 1861-0-0, NY; N Naruhashi 2567, A; CS Sargent 1892-9-26, A; H Takahashi et al. 6261, TUS-126291; C Wilford 1041, G, GH, K, NY.

HONSHU-OHWU: Aomori: PU Faurie 774, G; PU Faurie 5793, G (2); PU Faurie 5795, A, E; K Hosoi 2467, A; H Muroi 4608, A; T Naito 1971-6-8, A, E; S Okamoto 1963-9-8, MAK-40482; Akita: Y Endo 927, TUS-98395; T Makino 1927-0-0, MAK-50025, MAK-50092; Iwate: T Makino 1890-8-0, MAK-50022; H Muroi 3958, A; H Muroi 5738, A; Y Tateishi et al. 11194, E, TUS-129715; Yamagata: Mori 1955-8-16, MAK-7123; Mori 1958-5-14, MAK-19936; H Ohashi 6750, TI; K Uno 2612, A; Miyagi: H Muroi 4764, A; H Ohashi et al. 21863, E, TUS-121077; Y Takeuchi 1960-10-10, TUS-3238; Fukushima: HT Im & T Kawahara 7740, TI.

HONSHU-KANTO: Gunma: T Makino 1936-9-6, MAK-50034; Tochigi: EC Abbe et

al. 10065, A; J Bisset 1200, E; J Bisset 4318, E (2); JG Jack 1905-8-11, A; T Makino 1901-6-0, MAK-50036; T Makino 1901-10-0, MAK-50040, MAK-50041, MAK-50042; **Ibaraki**: MAK-50046; **Tokyo**: M Amano 31, TI; MAK-50051; **Kanagawa**: T Sawada 2360, TI; Collector unknown 1911-8-12, US-1176241. **HONSHU-CHUBU**: **Niigata**: PU Faurie 2491, G (2); T Nemoto 1522, TUS-90348; Y Tateishi et al. 8832, TUS-98916; M Togashi 7138, TI; T Yamazaki 1946-8-26, US-2037928; **Toyama**: S Kirino 819, US-2336335; G Murata 1976-6-6, TI; N Satomi 1963-5-12, MAK-30732; **Ishikawa**: T Fukui 1969-10-5, TUS-61380; H Furuike 1958-6-6, MAK-12148; N Satomi 5106, MAK-209586; **Fukui**: M Mutoh 24758, E, G, MAK-35834, NY; **Nagano**: DE Boufford & T Shimizu 23454, A, MICH; M Minemura 1961-8-10, MAK-17801; M Mizushima 1953-6-2, MAK-2027; M Ono & S Kobayashi 1965-7-22, MAK-134993; S Suzuki 1949-8-6&7, A;

HONSHU-KINKI: **Hyogo**: H Muroi 5437, A; **Shiga**: M Ito & A Iwami 3382, NY; **Osaka**: MAK-50020; **Nara**: M Hotta & N Fukuoka 243, MAK-35390, NY.

HONSHU-CHUGOKU: **Tottori**: H Muroi 5385, A; H Muroi 5386, A; H Muroi 5392, A; **Okayama**: K Oka 46936, TUS-95144; **Shimane**: Miyamoto 1959-8-10, MAK-15811; T Naito 1927-8-25, A;

FAGUS CRENATA BLUME SUBSP. **UNDULATA** (BUERGER) SHEN (JAPAN) (all collections examined)

HONSHU-KANTO: **Ibaraki**: S Kobayashi 3017, A; **Tokyo**: H Takeda 1904-7-6, E; **Kanagawa**: M Mizushima 703, A; M Mizushima 891, A.

HONSHU-CHUBU: **Yamanashi**: S Noshiro 2764, TUS-75440; **Shizuoka**: M Furuse

1952-6-13, A (2), E, G, MICH, NY, US-2211478; Y Kadota et al. 3634, A; G Murata 37207, MICH, NCU-514370; H Ohashi et al. 2041, A, NCU-516889, NCU-517109, TUS-65896.

HONSHU-CHUGOKU: Yamaguchi: K Ueda 68, TI.

SHIKOKU: Tokushima: G Murata et al. 56034, TI; Ehime: Collector unknown 1888-8-9, A; Kochi: M Yamanaka 1956-8-7, TUS-22376;

KYUSHU: Fukuoka: R Kanehira 1929-6-9, US-1529236; K Oka 47221, TUS-95135; Nagasaki: Sather & Caddell 3013, NCU-533235; Oita: J Murata 7970, TI-1315028; Kumamoto: Tagawa & Iwatsuki 3680, MAK-36176; Miyazaki: Sather & Caddell 2213, NCU-533233; Kagoshima: H Kanak... 9716, A; S Noshiro & M Suzuki 4840, TI; Z Tashiro 1917-5-19, A; EH Wilson 6240, A. Localities unknown: Collector unknown, sterile, GH (on the sheet of C Wright 1853-1856, a good fruiting collection of F. crenata subsp. crenata); Collector unknown, L-16907-76; Collector unknown, L-16907-77; Collector unknown, L-16907-78.

FAGUS SYLVATICA L. SUBSP. SYLVATICA (EUROPE) (selected fruiting collections examined unless otherwise indicated)

UNITED KINGDOM: WP Alcott 1877-7-13, A; RN Parker 1903-7-25, A; WB Turrill 1935-7-10, K;

NORWAY: R Collett 1867-8-16, K;

SWEDEN: E Nordstroem 1894-8-12, MICH; AO Olson 1920-8-12, G-66699;

BELGIUM: Lucion 553, G-167950;

FRANCE: D Aeschmann 2814, G-203072 (2); M Belanger 1823-7-0, G; SE

Lassimonne 1899-10-9, MU-19815; G Tour & E Jousset 4797, G (2); **Corsica:**
JW Harshberger 1189, US-1425462;
SPAIN: E Bourgeau 692, G; FR Fosberg 40921, US-2681415; A Rodriguez
1954-7-0, G;
DENMARK: J Ball 1888-9-5, US-683648; K Larsen 1967-6-17, G-10352;
GERMANY: J Bornmueller 1921-6-5, A; J Bornmueller 1931-8-0, A; L Holm-
Nielsen et al. 1974-8-9, A, G-133; AH Moore 4642, GH;
AUSTRIA: K Rechinger 1893-7-5, sterile, A;
SWITZERLAND: J Briquet 1920-8-10, G; J Briquet 1924-6-30, G; Chriss
1885-9-0, A; A Haller 1622, G; KU Kramer 5591, NCU-495688;
ITALY: TA Baldini 1890-9-14, G (2); PH Davis 47873, E, K; A Fiori 1911-
9-0, GH; G Sarfatti & A Contardo 1951-7-0, NCU-150382; **Sicily:** D Davis &
S Sutton 63898, E;
POLAND: F Krawiec 1938-6-8, G-34978, NCU-206857; E Panow 1934-6-0, US-
1629890;
CZECHOSLOVAKIA: G Rican 1931-6-30, G, WA;
HUNGARY: Z Debreczy & I Racz 9512, A; G Jermy s.n., US-369830;
YUGOSLAVIA: **Bosnia:** K Maly 1928-7-12, A; K Maly 1932-7-10, A; **Croatia:** D
Aeschimann 4026, G-265604 (3); HP Thompson 774, K; **Montenegro:** HP
Thompson 55, K;
ROMANIA: G Filip 1928-7-8, A; CC Georgesen 1934-9-0, G; CC Georgesen
1937-7-12, G; BVD Post 168, G; **Collections with rather typical**
vegetative characteristics of subsp. orientalis: D Cirtu et al. 1963-8-
16, G (2);
(MOLDAVIA): Arnaum 1964-7-8, E, G; **Collections with typical vegetative**
characteristics of subsp. orientalis: Ovanesova 1963-7-12, G;

UKRAINE-KRYM: Collections with (rather) typical vegetative characteristics of subsp. orientalis: Asmakhova 1957-7-27, fr., E; PH Davis 33402, st., E; PH Davis 33447, st., E, K; PH Davis 33472, st., E; G Poplavskaia 1926-0-0, st., A, G, MICH; CS Sargent 1903-7-13, fr., A; V Vasak 1977-7-30-a, fr., G-274539; Collections intermediate between subsp. sylvatica and subsp. orientalis in vegetative features: Asmakhova 1955-8-26, fr., E; Golde 1902-5-0 & -8-0, fr., WA; G Poplavskaia 1926-5-7 & -9-25, fr., A, G, MICH, WA; V Vasak 1977-8-1, fr., G-274538 (2); N Zelentskij 1885-7-0, st., G (2); Collections with rather typical vegetative characteristics of subsp. hohenackeriana: V Vasak 1977-7-30-b, st., G-274539;

BULGARIA (all fruiting unless indicated as sterile): D Antonov 1931-7-2, A; A Bialcheff 1932-6-9, A; I Bondev et al. 1975-6-3, 1,600 m alt., E, G-110850; E Bozhilova 1961-4-22, WA; Z Debreczy & I Racz 1979-9-4, 1,400 m alt., A; B Kitanov 1951-6-15, G; S Kozhuharov & A Petrova 1975-5-29, E, G-110851; J Mattfeld 4360, 450 m alt., A; J Mattfeld 4361, 450 m alt., A; Stefanov & Ruskov 1928-5-8-b, A; N Stojanov 1928-6-10-a (=B Stefanov 1928-6-10, A), GH, US-1429004; N Stojanov 1929-6-29, A; N Stojanov & B Stefanov 1928-5-12, A; L Tanimadjiev 1931-8-20, A; L Tanimadjiev 1931-9-1, A; L Tanimadjiev 1931-9-10, A; WB Turritt 1431, 1,400 m alt., K; Collections intermediate between subsp. orientalis and subsp. sylvatica in vegetative features: N Stojanov 1928-6-10-b, GH, US-1429004; Collections with (rather) typical vegetative characteristics of subsp. orientalis: Z Cherneva & P Gerginov 1975-5-20, E, G-110849; Collections with rather typical vegetative characteristics of subsp. hohenackeriana: N Vichodcevsy 1955-7-20, sterile, G;

GREECE (all fruiting unless indicated as sterile): L Bernardi 1977-7-0, G (6); PH Davis 47861, 1,500 m alt., E; O Dibowski 1928-7-1, 1,600 m alt., G; W Greuter et al. 15186 (= A Charpin 14495), 1,150 m alt., G-171021 (2); P Hartvig & O Seberg 4415, 1,400 m alt., G-188211; T Heldreich 1882-8-7, 900-1,200 m alt., G; J Mattfeld 2600, A; J Mattfeld 3011, A; C Regel 1934-8-24-a, 1,300 m alt., G (2); C Regel 1936-7-6-b, G; C Regel 1939-7-8-a, G; P Sintenis 958, E, G; A Strid 15719, 1,400-1,600 m alt., G; Strid & Papanicolaou 16112, 1,650-1,800 m alt., G-174013; Strid & Papanicolaou 16537, 1,400-1,700 m alt., G-170456; HG Tedd 1934-7-22, 1,500 m alt., K (2); Topali 1936-9-18, 1,200 m alt., G; Collections intermediate between subsp. orientalis and subsp. sylvatica in vegetative features: W Greuter 11381, 1,250 m alt., G-65245; KH Rechinger 10327, 750-1,500 m alt., G; Collections with (rather) typical vegetative characteristics of subsp. orientalis: P Hartvig & A Strid 24234, G-283702; J Mattfeld 3091, 1,000 m alt., sterile, A, US-1430609; J Mattfeld 3092, 1,000 m alt., sterile, A, US-1430610; J Mattfeld 3114, 1,295 m alt., A (3, one fruiting, two sterile); KH Rechinger 15414, 900-1,100 m alt., G; C Regel 1938-8-12-a, sterile, G; C Regel 1938-8-12-b, sterile, G; C Regel 1938-8-12-c, sterile, G; C Regel 1938-8-12-d, sterile, G (2);

FAGUS SYLVATICA L. SUBSP. ORIENTALIS (LIPSKY) GREUTER & BURDET (W EURASIA) (all collections examined)

TURKEY (Al): **Kirklareli:** A Baytop 1968-6-12 (=ISTE-13236), fr., E; A

Baytop 1968-6-12 (=ISTE-13288), fr., A; J Mattfeld 3479, fr., A; J Mattfeld 3484, fr., A; J Mattfeld 3781, fr., A; J Mattfeld 3808, st., A; Balikesir: Kayacik & Yaltirik 1965-5-12 (=ISTO-3272), st., E;

TURKEY (A2): Istanbul: GV Aznavour 1889-8-29, fr., G; GV Aznavour 1890-9-29, fr., G; GV Aznavour 1894-9-23, st., G; GV Aznavour 1895-6-3, fr., G; GV Aznavour 1905-8-6, st., G; EK Ball 2387, fr., A, E; J Bornmueller 13555, fr., A; J Mattfeld 3212, fr., A; B Kuzmanov 77847, fr., G-147462; C Regel 1956-7-8, st., G; **Bursa:** E Burnat 1889-6-6, fr., G; Z Debreczy & I Racz 1980-10-1, st., A; E Murray 954, st., E; O Polunin 15047, fr., E; WR Prue 712, st., K; C Regel 1931-8-3, st., G; C Regel 1932-7-7-a, st., G; C Regel 1932-7-7-b, st., G; C Regel 1932-7-7-c, st., G; C Regel 1932-7-7-d, st., G; C Regel 1963-7-9, st., G; Steetz 463, fr., G;

TURKEY (A3): Adapazari: Davis & Coode 39114, st., E; **Bolu:** A Charpin 19989, fr., G-288306; G Cobham 103, fr., K; Davis & Hedge 32868, fr., E; BVD Post 1940-7-13, fr., G; KH Rechinger 15308, fr., G; P Uotila 15532, st., E; **Zonguldak:** PH Davis et al. 37539, st., E; C Regel 1956-5-16-a, st., G; C Regel 1956-5-16-b, st., G;

TURKEY (A4): Zonguldak: PH Davis et al. 37622, fr., E; **Kastamonu:** PH Davis 38606, st., E; P Sintenis 3715, fr., NY; P Sintenis 5113, fr.,

TURKEY (A5): Sinop: PH Davis et al. 38226, fr., E; **Amasya:** Manissadjian 369-b, fr., E, G;

TURKEY (A6): Samsun: C Tobey 782, fr., E; **Ordu:** Davis & Polunin 24935, fr., E; C Tobey 1394, st., E;

TURKEY (A7): Giresun: PH Davis et al. 20493, st., E; **Trabzon:** EK Balls 1624, st., A, E, K (2), US-2318861;

TURKEY (A8): Trabzon: Stainton 8408, fr., K; **Coruh:** Davis & Hedge 32347-

b, fr., E;

TURKEY (B1): Canakkale: C Regel 1964-6-10, st., NC-413615; **Balikesir:** P Sintenis 581, st., A, E, G;

TURKEY (B2): Bursa: Davis & Coode 36655, st., E; **Kutahya:** MJE Coode & BMG Jones 2647, st., A, E; MJE Coode & BMG Jones 2668, fr., A, E, K; PH Davis 18492, fr., E; Davis & Coode 36837, st., E;

TURKEY (B3): Eskisehir: T Ekim 489, st., E;

TURKEY (C6): Adana: HJ Beug & G Wagenitz 402, st., E; PH Davis 16398, fr., E; PH Davis 16443, st., E, G-250509 (2); Davis & Hedge 26880, st., E; M Haradjian 3684, fr., G; **Kahramanmaras:** MJE Coode & BMG Jones 1210, st., A, E, K; Kayacik s.n. (=ISTO-546), st., E; **Localities unclear or unknown:** U Delbes 1935-11-0, st., G; U Delbes 103, fr., G (2); M Haradjian 2489, fr., G; M Haradjian 2668, fr., G; BVD Post 1884-9-18, fr., G, US-805110;

TURKEY-Localities unknown: NE Turkey, Steetz 529, fr., G;

RUSSIA: Krasnodar: N Bush 1897-7-14, fr., A;

GRUZIJA: EE Gogina 1971-6-19-a, fr., A, E, NC-470557; EE Gogina 1971-6-19-b, fr., G; YS Medvideva 1902-5-7, fr., A; T Mlonosicssicz 1903-8-26, fr., WA; A Somakin 1920-4-0, fr., A; V Vasak 1979-7-9-a, fr., G-213371 (2); V Vasak 1979-7-9-b, fr., G-299498 (2); V Vasak 1980-7-18, fr., G-299497; **Localities unclear:** N Albov 18, G (3);

AZERBAJDZHAN: M Brzhezitzky & M Kasumov 1933-8-4, fr., A; II Karjagina 1928-7-9, fr., A;

CAUCASIA-localities unknown or unclear: K Malsalskij s.n., fr., A; B Marcowicz s.n., G;

IRAN: Gilan: N Lindsay 1051, fr., K;

BULGARIA: E Bozhilova 1965-8-9, st., WA; HM Burdet & A Charpin 10055, fr., G; PF Olsen 1151, fr. G-201296; Ruskov 1928-5-8, fr., GH, US-1429008; Stefanov & Ruskov 1928-5-8-a, st., A; CK Schneider 598, fr., A; V Stojanov & B Stefanov 1925-8-8, fr., A; N Stojanov 1925-8-14, fr., A; WB Turrill 900, fr., K; WB Turrill 1450, st., K (2); WB Turrill 1472, st., K; WB Turrill 1483, st., K; WB Turrill 1713, st., K (2); T Wisniewski 2257, st., MICH; NB Vychodcevski 1917-7-6, st., G;

GREECE: PH Davis 47833, fr., E;

ROMANIA: Collections intermediate between subsp. sylvatica and subsp. orientalis in vegetative features: S Pascovschi 1946-6-5, fr., G;

FAGUS SYLVATICA L. SUBSP. HOHENACKERIANA (PALIBIN) SHEN (W EURASIA)
(all collections examined)

IRAN: Mazanderan: JR-789, fr., G; B Kasapligil 2791, fr., G; KH Rechinger 2006, st., US-2061555; D Walton 242, st., E; D Walton 243, st., E; **Gilan:** T Alexeenko 1902-7-17, fr., A; J Lamond 2966, st., E; J Lamond 5136, fr., E; KH Rechinger 39741, st., G-79464; KH Rechinger 43402, fr., G-79465; **Collections with (rather) typical vegetative characteristics of subsp. orientalis:** Aucher 5325, fr., G; Serv. For. Iran SF-02, fr., G (2);

AZERBAJDZHAN: T Alexeenko 1900-7-21 & -8-3, A (fr.), G (3, fr. & st.); **NV Shipchinskij** 1185, fr., WA-30788; **Talysh:** Bush 801, fr., A; A Koffod 1898-7-7, fr. NY; N Pastuchov 1914-9-24, fr., NY;

ARMENIA: TS Elias 3133, fr., NY; A Fomine 1900-5-14, st., A; W Greuter

12766, fr., E, G-102837; V Manakjan 1960-7-6, st., E; V Vasak 1974-10-5-a, st., G-146362; V Vasak 1974-10-5-b, st., G-299493; V Vasak 1974-10-5-c, st., G-299499;

GRUZIJA: N Albov 524, fr., G; V Kozlovskij 1917-8-31, fr., NY; Munyniski 1916-7-27, WA; N Pastuchov 1917-9-17, fr., NY; Sodvadze 1976-6-17, seedlings, NY; V Vasak 1976-6-14-a, st., G-274537 (2); V Vasak 1976-6-14-b, st., G-299494; V Vasak 1977-6-21, st., G-299479; V Vasak 1981-6-16, st., G-299495; V Vasak 1982-7-31, st., G-299482; V Vasak 1982-8-3, st., G-299480; **Collections with (rather) typical vegetative characteristics of subsp. orientalis:** N Albov 2, fr., G (2); PN Krylov & EI Shtejnberg 1916-6-29, fr., A; S Kutateladze et al. 1959-8-29, fr., E; S Sommier & E Levier 1890-6-16, fr., G; V Vasak 1979-7-12, fr., G-299481 (2); V Vasak 1979-7-26, fr., G-299477 (2); V Vasak 1980-7-13, fr., G-299483;

RUSSIA: Krasnodar: NA Bush & EA Bush 1908-5-14, fr., A; TS Elias 6477, fr., NY; TS Elias 6564, fr., NY; N Kuznetsov 1888-7-26, st., NY; M Mich... 1923-7-20, st., GH; V Vasak 1976-6-10-a, st., G-274535; V Vasak 1976-6-10-b, st., G-299478 (2); V Vasak 1976-6-15, st., G-276522; V Vasak & A Vezda 1978-6-8, st., G-274534; V Vasak & A Vezda 1978-6-16, st., G-231536; V Vasak 1979-6-16, st., G-299029 (2); V Vasak 1980-6-30, st., G-299496 (2); Collector unclear 1958-5-25, fr., NY; Collector unknown, st., A; **Balkar:** EA Bush & NA Bush 1927-7-17, st., G; **Severo-Osetin:** EA Bush & NA Bush 1927-8-16, st., G; B Marcowicz 1898-4-0 & -7-0, fr., A, E (3), G (3), GH, WA; **Circassia:** B Hryniewiecki 1901-6-0, fr., A; **Chechen-Ingush:** I Akinfiev 1898-8-28, fr. G, WA; **Collections with (rather) typical vegetative characteristics of subsp. orientalis:** V

Vasak 1979-6-22, fr., G-274536 (2);

CAUCASIA-Localities unknown or unclear: IP Petrova 1901-8-16, st., A; CS Sargent 1903-7-19, fr., A; Hohenacker s.n., fr., E, G (2), US-254305;

TURKEY (A9): Coruh: Tong 504, st., E;

TURKEY (A8): Coruh: Davis & Hedge 32347-a, fr., E; Rize: Davis & Dodds 21285, st., E; E Murray 934, st., A, E; Collections with rather typical vegetative characteristics of subsp. orientalis: Davis & Dodds 21380, fr., E;

FAGUS GRANDIFOLIA EHRH. SUBSP. GRANDIFOLIA (CANADA & THE UNITED STATES OF AMERICA) (Selected typical fruiting collections. All examined fruiting collections from these provinces and states are assignable to subsp. grandifolia unless otherwise indicated.)

CANADA-PRINCE EDWARD ISLAND: ML Fernald et al. 7311, A, GH; CS Sargent 1895-8-16, A;

CANADA-NOVA SCOTIA: ML Fernald & CH Bissell 21023, A, GH; ML Fernald et al. 23783, A; JG Jack 3497, GH; B Long & DH Linder 21025, GH; EC Smith et al. 18944-a, MU-122878;

CANADA-NEW BRUNSWICK: MA Chrysler 6355, GH;

CANADA-QUEBEC: PF Maycock 1962-9-29, MICH; JG Jack 1895-8-26, A; B Rolland-Germain 1946-7-26, E, GH, NC-200070, TENN, US-2328132; F Rolland-Germain 2350, GH, US-2313558;

CANADA-ONTARIO: JA Calder 2435, E; J Fowler 1892-7-28, US-261111; JH Soper 2664, GH; LM Umbach 1899-7-7, US-382995;

USA-MAINE: RC Bean 1934-8-4, NEBC; NC Fassett 13412, MU-19809; ML Fernald 1894-8-11, A; ML Fernald 1894-9-1, A; RC Friesner 24495, GH; AF Hill 1818, NEBC; CH Knowlton 1909-7-14, NEBC (2);

USA-NEW HAMPSHIRE: CF Batchelder 1920-7-8, NEBC; Oakes s.n., GH; AH Moore 4046, GH; AS Pease 16497, NEBC; A Rehder 996, A; BL Robinson 1897-7-12, GH; AF Stevens 1895-9-20, US-311782; EF Williams 1895-7-15, GH;

USA-VERMONT: CG Pringle 1879-10-2, US-930813; FC Seymour 3448, NEBC; AF Stevens 1892-7-0, US-311783; LA Wheeler 112502, NEBC; LA Wheeler 112603, NEBC; EW Wood & DE Boufford 4727, A;

USA-MASSACHUSETTS (some examined fruiting collections from the state are close to subsp. caroliniana): JR Churchill 1904-6-28, NEBC; MA Day 18, GH; LH Elwell 1891-7-11, NEBC; ML Fernald & B Long 18361, NEBC; BN Gates 25061, NEBC; CH Morss 1901-6-17, NEBC; EF Williams 1907-7-13, GH;

USA-RHODE ISLAND: EJ Palmer 44649, A; CS Sargent 1879-8-0, A; G Thurber 1844-5-0, GH;

USA-CONNECTICUT (some examined fruiting collections from the state are close to subsp. caroliniana): D McKeurin 185, NEBC; CA Weatherby 1732, NEBC; CA Weatherby 1914-6-21, NEBC;

USA-NEW YORK (some examined fruiting collections from the state are assignable to subsp. caroliniana): GR Cooley 12171, MU-110893; ML Fernald et al. 14252, GH; WE Manning 1922-7-29, NCU-352196; WA Matthews 3203, NCU-29891; WA Murrill 1889-7-1, ECON-22141, GH; H St.John 2690, GH;

USA-MICHIGAN (a few examined fruiting collections from the state are assignable to subsp. caroliniana): BF Chandler 1917-6-17, US-984431; CK Dodge 1896-5-10, TENN; R Garlitz 400, MICH; RH Read 197, MICH; EG Voss

10974, MICH;

USA-WISCONSIN: G Goff 1964-6-23, NCU-330213; HH Iltis 21777, NCU-381389;
JH Schuette 122, US-751826;

FAGUS GRANDIFOLIA EHRH. SUBSP. CAROLINIANA (LOUDON) CAMP EX SHEN (THE UNITED STATES OF AMERICA) (Selected typical fruiting collections. All examined fruiting collections from these states are assignable to subsp. caroliniana unless otherwise indicated.)

TEXAS: WW Ashe 1921-10-20, NCU-23910; GL Fisher 1931-6-20, MU-131726;
Lundell & Lundell 10500, MICH; EJ Palmer 12731, A, GH;

LOUISIANA: WW Ashe 1921-10-10, NCU-23904; CM Allen 8301 (= K Vincent 1445), NCU-497081; CA Brown 7745, A; D Demaree 48209, GH; RD Thomas et al. 10786, NCU-328447; RD Thomas 21443, MICH; JW Thieret 23917, US-2526393; K Vincent 2705, NCU-509007;

MISSISSIPPI: GR Cooley 4997, GH; SB Jones 7589, NCU-273845; SB Jones 16236, NCU-357970; SB Jones 17577, NCU-357896; R McVaugh 8505, MICH; KE Rogers 45186, TENN;

ALABAMA: RC Clark 5637, NCU-353902; RC Clark 8999, NCU-353919; RC Clark 16971, NCU-353948; J Weaver 144, NCU-385408;

FLORIDA: H Foster 8222, A, MICH, US-1730428; GV Nash 2339, A, E, MICH, NCU-23906;

GEORGIA: WH Duncan 3096, GH, NCU-24475, TENN; WH Duncan 5585, NCU-258882; WH Duncan 8373, GH, US-2579125; WR Faircloth 5757, NCU-395104;
WR Faircloth 7366, TENN; JE Fairey 761, NY; EW Wood & DE Boufford 1703,

NCU-477417;

SOUTH CAROLINA: HE Ahles 34350, NCU-154684; CR Bell 8549, NCU-154924; CR Bell 10108, NCU-154903; AE Radford 26688, NCU-154699; AE Radford 26948, NCU-167342; CL Rodgers & NE Mullens 67129, NCU-297157; BE Smith 1235, NCU-25842;

NORTH CAROLINA (some examined fruiting collections from the state are assignable to subsp. grandifolia): HE Ahles 15062, NCU-154700; HE Ahles 16493, NCU-154696; HE Ahles 20048, NCU-154701; HE Ahles 44699, NCU-154704; HE Ahles 48869, NCU-154715; HE Ahles 52307, NCU-154708; H Laing 1552, NCU-154714; AE Radford 40554, NCU-154693;

TENNESSEE (some examined fruiting collections from the state are close to subsp. grandifolia): WB McDougall 1451, US-1925084; RE Shanks et al 14931, NCU-324177; RE Shanks 26943, GH; AJ Sharp et al. 3688, NCU-242386; AJ Sharp et al. 4227, NCU-240466; AJ Sharp et al 5743, NCU-242384; AJ Sharp et al. 7956, NCU-240469; AJ Sharp et al. 9440, NCU-324180;

ARKANSAS: D Demaree 12974, GH; D Demaree 37382, GH; D Demaree 47987, TENN; D Demaree 57149, NCU-344127, TENN; DM Moore 43-222, NCU-292956; EJ Palmer 8076, A; EJ Palmer 29268, A;

MISSOURI: BF Bush 6259, A; BF Bush 6393, A, GH, US-671948; H Eggert 1894-5-20, A; JH Kellogg 25850, A; JH Kellogg 27037, A;

FAGUS GRANDIFOLIA EHRH. SUBSP. MEXICANA (MARTINEZ) CAMP EX SHEN (MEXICO) (all collections examined)

TAMAULIPAS: Gomez Farias: BE Harrell 250, st., TENN; F Gonzalez-Medrano et al. 2492, st., MEXU-152565; PS Martin H-27, fr., MICH; H Puig 7219, fr., MEXU-391209; AJ Sharp 50-172 (= E Hernandez-Xolocotzi 5912, MEXU-49415), st., MEXU-153738, TENN; AJ Sharp 52-106 (= E Hernandez-X 8046, n.v.), fr., GH, NY, TENN;

HIDALGO: Mojonera (= Zacualtipan): M Martinez 1939-0-0, fr., US-1748886; M Martinez 1939-8-10, fr., GH; M Martinez 1939-9-0, fr., A; M Martinez 1940-8-0, fr., GH; M Martinez 1941-2-2, fr., G (2), NY, US-1792875, US-1792876; M Martinez 800, fr., A (2), US-1749597; M Martinez 1500, fr., MEXU-9631; M Martinez 1650, fr., MEXU-9507, MEXU-9945, MEXU-9546; M Martinez 1800, fr., MEXU-9508; F Miranda 3243, st., MEXU-66293; HE Moore 3348, st., MICH, US-1945934; R Moran 10070, st., US-2401654; R Peters 1989 7/8, st., NY; R Peters 1990-1/2, st., NY; J Rzedowski 12551, st., MICH; J Rzedowski 29461, fr., MICH; AJ Sharp 46-227, st., MEXU-136721, TENN; AJ Sharp 46-229, st., GH, MEXU-135992, TENN; **Tutotepec:** F Miranda 3748, fr., MEXU-67073; AJ Sharp 45-859, fr., GH, MEXU-136708, NY, TENN (2); AJ Sharp 46-169, fr., GH, NY, TENN; AJ Sharp 46-170, GH, MEXU-136860; AJ Sharp 46-171, st., TENN;

PUEBLA: Teziutlan: W Boege 2124, st., MEXU-94897; WB Fox 5828, st., TENN; R Hernandez-M 308, st., MEXU-114225;

VERACRUZ: Jalapa: R Peters 1989-10-12, st., NY;

APPENDIX 3

PLATES

PLATES 1-2: TREE-SHAPE OF SUBGENUS ENGLERIANA AND BARKS OF FAGUS

(All are taken from trees cultivated in the Arnold Arboretum, Jamaica Plain, Massachusetts, USA. All close-ups of barks are roughly of the same magnification)

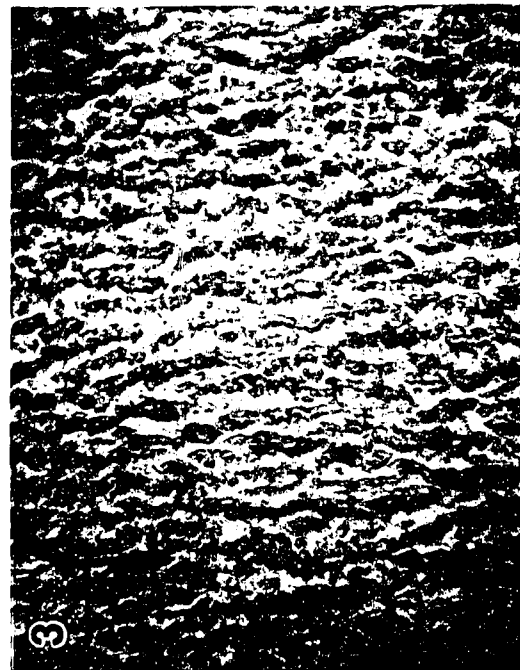
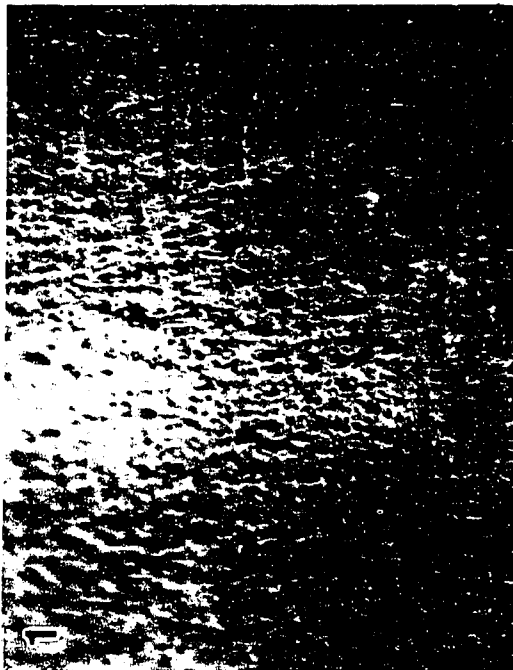
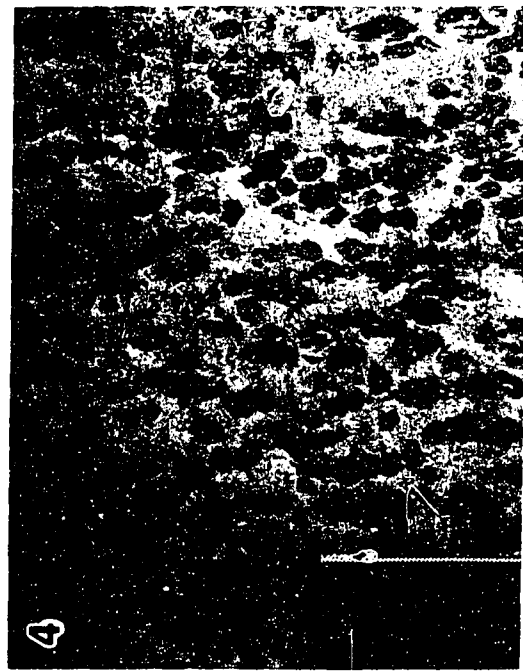
PLATE 1: TREE-SHAPE AND BARK OF SUBGENUS ENGLERIANA

- 1: F. engleriana, cult. in Arnold Arb., # 383-27-B.
- 2: F. engleriana, same as above.
- 3: F. japonica, cult. in Arnold Arb., # 14587-B.
- 4: F. japonica, same as above.



PLATE 2: BARK OF SUBGENUS FAGUS

- 1: F. lucida, cult. in Arnold Arb., # 7418-A.
- 2: F. crenata subsp. crenata, cult. in Arnold Arb., # 2122-C.
- 3: F. sylvatica subsp. hohenackeriana, cult. in Arnold Arb.,
14586-1
- 4: F. grandifolia, wild in Arnold Arb.



PLATES 3-14: REPRESENTATIVE OR PECULIAR COLLECTIONS

(All are of the same reduction rate, except Pl. 9, Fig. 1)

PLATE 3: F. ENGLERIANA AND F. JAPONICA SUBSP. ANGUSTIFOLIA

- 1: F. engleriana, CS Chang 121, KOREA-Ulreung-Do, 350 m, very wet habitat, (NY). [Sterile. Rather typical sterile leaves, only very slightly glaucous.]
- 2: F. engleriana, CS Chang 136, KOREA-Ulreung-Do, 300 m, very open habitat, (NY). [A rather typical fruiting collection. Very conspicuously glaucous leaves. Note the shape of cupule-valves, and the tiny but clear triangular extensions very close to the nut-tip.]
- 3: F. engleriana, Elsik & Erwin 1957, cult. in (A), AA-383-27-B, from CHINA-Hubei, (A). [Leaves a bit too slender, rarely seen. Note the more downward-extended narrow nut-wings.]
- 4: F. japonica subsp. angustifolia, Michener & Bennett 1974, cult. in (A), source unknown, (A). [TYPE. Note the narrowing-down lower margin, compare this point with all other photographed collections of the same subgenus.]

PLATE 4: F. JAPONICA SUBSP. JAPONICA AND F. OKAMOTOI

- 1: F. japonica subsp. japonica, J Bisset 4256, JAPAN-Honshu-Tochigi-Nikko, (E). [A rather typical fruiting collection. Note the long whitish hairs on major veins and even on the non-venous surface, and that the nuts are about twice as large as the cupule-valves.]
- 2: F. japonica subsp. japonica, Tateishi & Chen 10237, JAPAN-Honshu-Fukushima-Iwase, 600-800 m, (TUS-99724). [Note the nearly rhombic leaves characterizing this collection. They represent another prevailing leaf-type of this taxon.]
- 3: F. okamotoi, Hara & Ohashi 1970-7-23, JAPAN-Honshu-Tochigi-Nikko, (TUS-63872). [The leaves of this collection are perhaps biologically more typical for this species.]
- 4: F. okamotoi, S Noshiro 1606, JAPAN-Honshu-Yamanashi-Enzan, 1,420 m, (TUS-75454). [TYPE. Note the small and strongly winged nuts.]

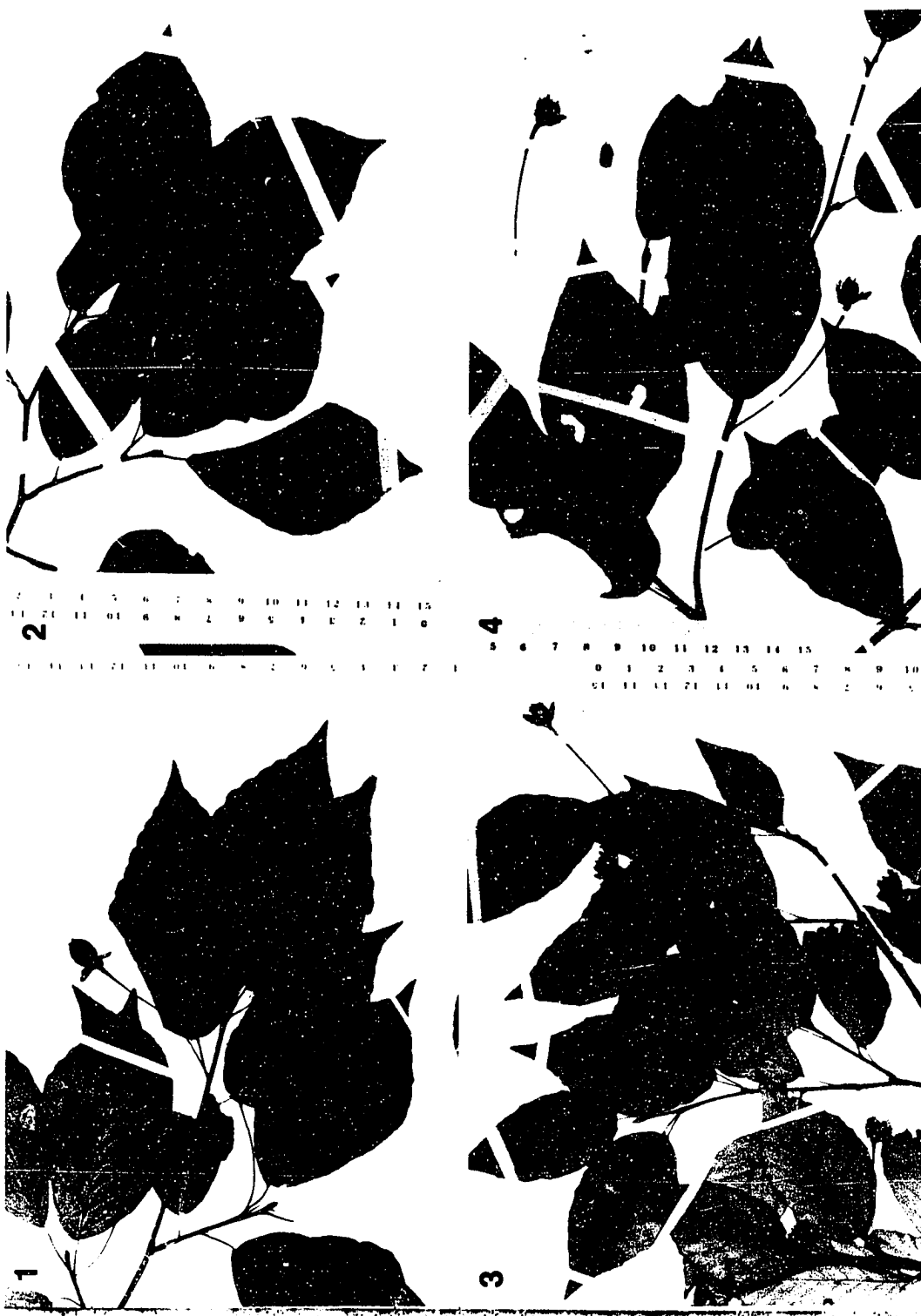


PLATE 5: F. LONGIPETIOLATA

- 1: Sino-Am 1986 Gueizhou Exp. 1304, CHINA-Gueizhou-Injiang-(Fanjingshan), 850-1,300 m, (NY). [Note the leaf at the left, both its shape and margin are not very frequently seen. Note the shorter but still clearly thread-like basally-borne appendages.]
- 2: AN Steward et al. 190, CHINA-Guangxi-Lingyun-Nakan, 1,360 m, (A). [On the average a rather typical collection, with immature cupule/nut complex.]
- 3: CL Tso 20560, CHINA-Guangdong-Lechang, (NY). [Perhaps rather representative for populations growing on more wet habitats.]
- 4: YW Taam 738, CHINA-Guangdong-Xinfeng-Chaping, (A). [Very rarely seen leaves, only found in this locality. They are too small, with too much reduced serration, too few lateral veins, acute rather than acuminate apex, ovate rather than long-ovate to long-oblong in shape, with too dense and too chemically active glandular hairs. All these are atypical for this taxon. However, this individual looks alright in other respects.]

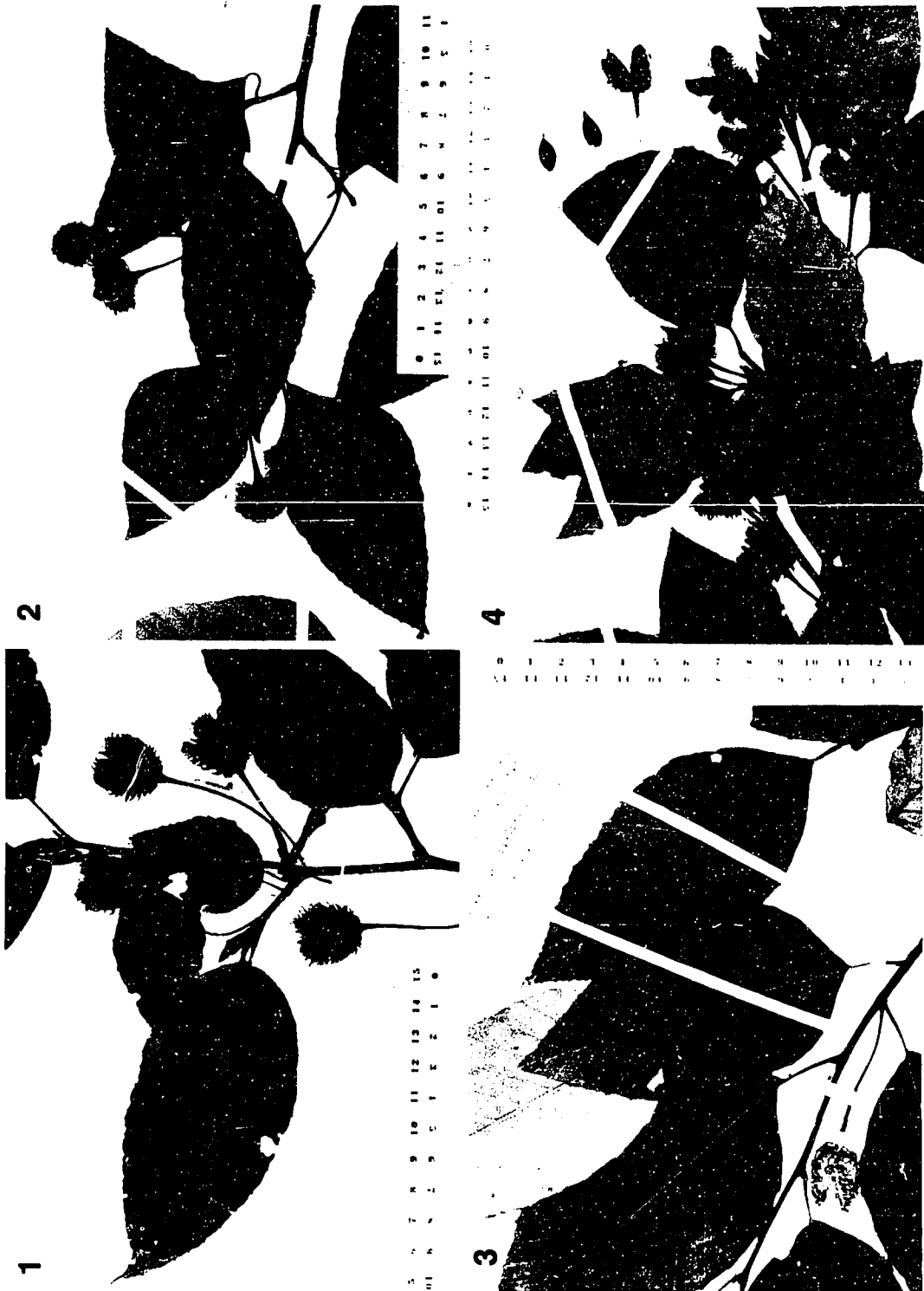


PLATE 6: F. LONGIPETIOLATA, F. BREVIPETIOLATA, F. BIJIENSIS, AND
F. TIENTAIENSIS

- 1: F. longipetiolata, RC Ching 3216, CHINA-Jiangxi-Wuyuen-
(Zhanggongshan), 700 m, (A). [Form perhaps more common in the
eastern range of the species, unusually broad.]
- 2: F. brevipetiolata, JW Ge 1988-10-27, Population 2-3, CHINA-
Sichuan-Nanjiang-Weijiahe, 1,450 m, sprout, 2.5 m tall, sterile,
(NY). [Typical. Compare its bud with those of all other
photographed taxa of the same section.]
- 3: F. bijiensis, PH Yu 766, CHINA-Gueizhou-Bijie, 1,450 m, (IBSC-
343516). [TYPE. Note the elliptic to oblong nuts.]
- 4: F. tientaiensis, S Chen 3718, CHINA-Zhejiang-Tientai, (A).
[TYPE. Note its elliptic-oblong leaves.]

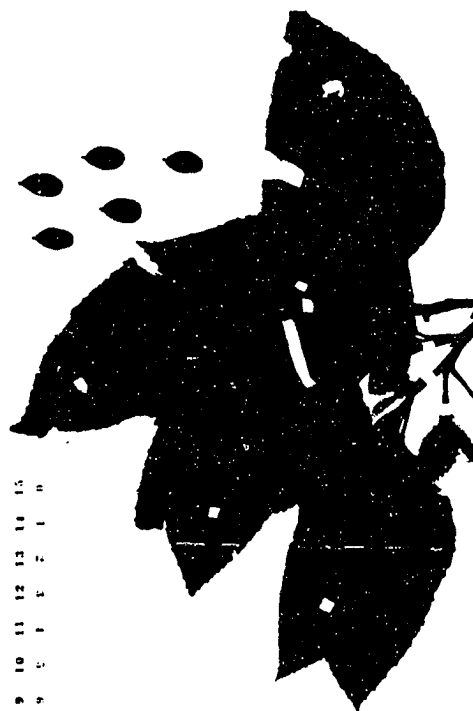
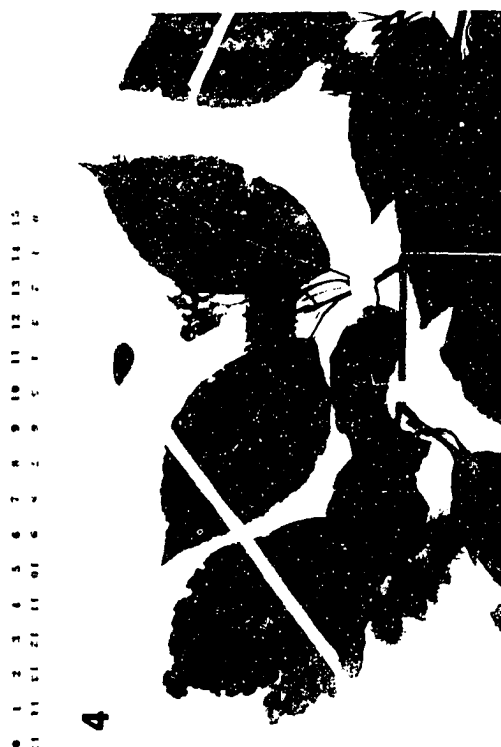
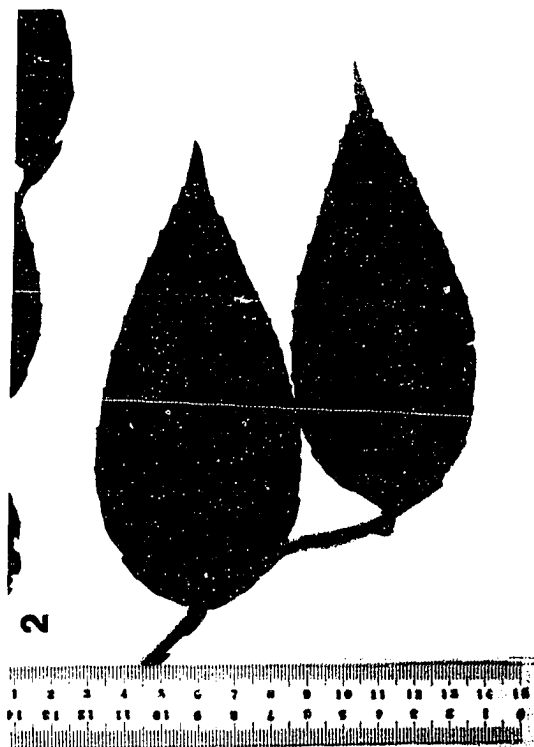


PLATE 7: F. LUCIDA AND F. CHIENII

- 1: F. lucida, AN Steward et al. 662, CHINA-Gueizhou-(Fanjingshan), 1,400-1,700 m, (NY). [Note the oblong and plump nuts. Note the characteristic leaf-shape, leaf-base, leaf-apex, and leaf-margin configuration. Particularly note the nearly straight to simply slightly curved base-margin, which is almost parallel to the basalmost lateral vein; and that the notch formed by the upper (or apical) side of the basalmost tooth and the basalmost intersecondary margin-section is characteristically slightly larger than the upper ones. All these leaf features are expressed very similarly in the following two collections. Note the 3-valved cupules, and the one bearing two half-fused valves and two unfused "normal" valves.]
- 2: F. lucida, Sino-Am 1980 W Hubei Exp. 1479, CHINA-Hubei-Shennongjia, 2,000 m, (NY). [Leaves too large, too broad, and too thin, looking like those on sterile shoots. No biologically attached cupules. Note the slightly yellowish/grayish current-year shoot - typical for the species. Particularly note the 3-valved/1-nutted cupule atop a rather slender and rather long (for the species) peduncle, the much reduced cupule-appendages, and the atypical nut. Deserving a subspecies ?]
- 3: F. lucida, HJ Li 6339, CHINA-Hubei-Hefeng, 1,230 m, sterile, (PE-737882). [A rather typical sterile collection.]
- 4: F. chienii, WC Cheng 2903, CHINA-Sichuan-Pingwu, 1,300 m, (A, IBSC, US). [TYPE. Note the oblong nuts, some of which bear

small extensions along the upper nut-angles. Note the slightly yellowish/grayish current-year shoot. Particularly note the leaf-shape, leaf-apex, leaf-margin configuration, and the outline of the lower portion of leaves - all are different from F. lucida.]



PLATE 8: F. HAYATAE SUBSP. PASHANICA

- 1: A Henry 6793, CHINA-Hubei-Fang, 2,100-2,850 m, 6 m tall, sterile, (IBSC-344388). [Note the differences between F. lucida and F. hayatae subsp. pashanica in leaves, as observed on their seven collections photographed here. This sterile collection is among the ones easily misidentified as F. lucida. In my concept, all expressions of gross-features in all leaves of this collection are compatible with those typical for F. hayatae subsp. pashanica. See below.]
- 2: CC Yang 75011, CHINA-Sichuan-Nanjiang, (ZJFC). [TYPE. Note the oblong to elliptic, smaller, and fewer-veined leaves. Particularly note the outline of the lower leaf-margin - similar to that of F. lucida, but the notch already pointed out for F. lucida tends to be slightly more prominent here - a characteristic for this subspecies ! Also note the configuration of leaf-margin - not found in F. lucida, but also common in subsp. hayatae.]
- 3: Sino-Am 1980 W Hubei Exp. 1485, CHINA-Hubei-Shennongjia, 2,050 m, 4 m tall, (NY). [Similar to subsp. hayatae. This configuration of leaf-margin is also common in subsp. hayatae.]
- 4: YK Hsiung 5852, CHINA-Hunan-(Mufushan), (A). [Typical leaves for subsp. pashanica. Peculiar in its much reduced cupule-appendages.]



PLATE 9: F. HAYATAE SUBSP. HAYATAE AND F. CRENATA SUBSP. UNDULATA

- 1: F. hayatae subsp. hayatae, Hsieh & Hsiao 1988-9-7, population sample, CHINA-Taiwan-Taipei-(Lupeishan), 1,400 m, sterile, (NY); the leaf on the right (indicated by an arrowhead) is a F. lucida, cult. in (A), AA-7418-A, from CHINA-Hubei, sterile. [Note the larger scale of this figure. It is x 15/9 larger. The central leaf is too large for the subspecies. Compare these five leaves of F. hayatae subsp. hayatae with the leaf of F. lucida at the right-hand side of this plate and the leaves of F. lucida on Pl. 7, Fig. 3, and the leaves of F. hayatae subsp. pashanica on Pl. 8, Fig. 1. All of them are on sterile shoots produced in lean-year.]
- 2: F. crenata subsp. undulata, Buerger s.n. (L-16907-77), JAPAN, (L). [Sterile. TYPE. Note the persistent stipules and the small leaves of this and the following two collections. The leaf-shape of this collection is very rarely encountered in subsp. crenata, but it is normal for subsp. undulata as defined here. Also note the undulate leaf-margin of this type collection.]
- 3: F. crenata subsp. undulata, M Furuse 1952-6-13 (= Exsiccata NSM-539), JAPAN-Honshu-Shizuoka-Ashitakayama, (A). [A rather typical collection.]
- 4: F. crenata subsp. undulata, K Oka 47221, JAPAN-Kyushu-Fukuoka, (TUS-95135). [Rather typical.]

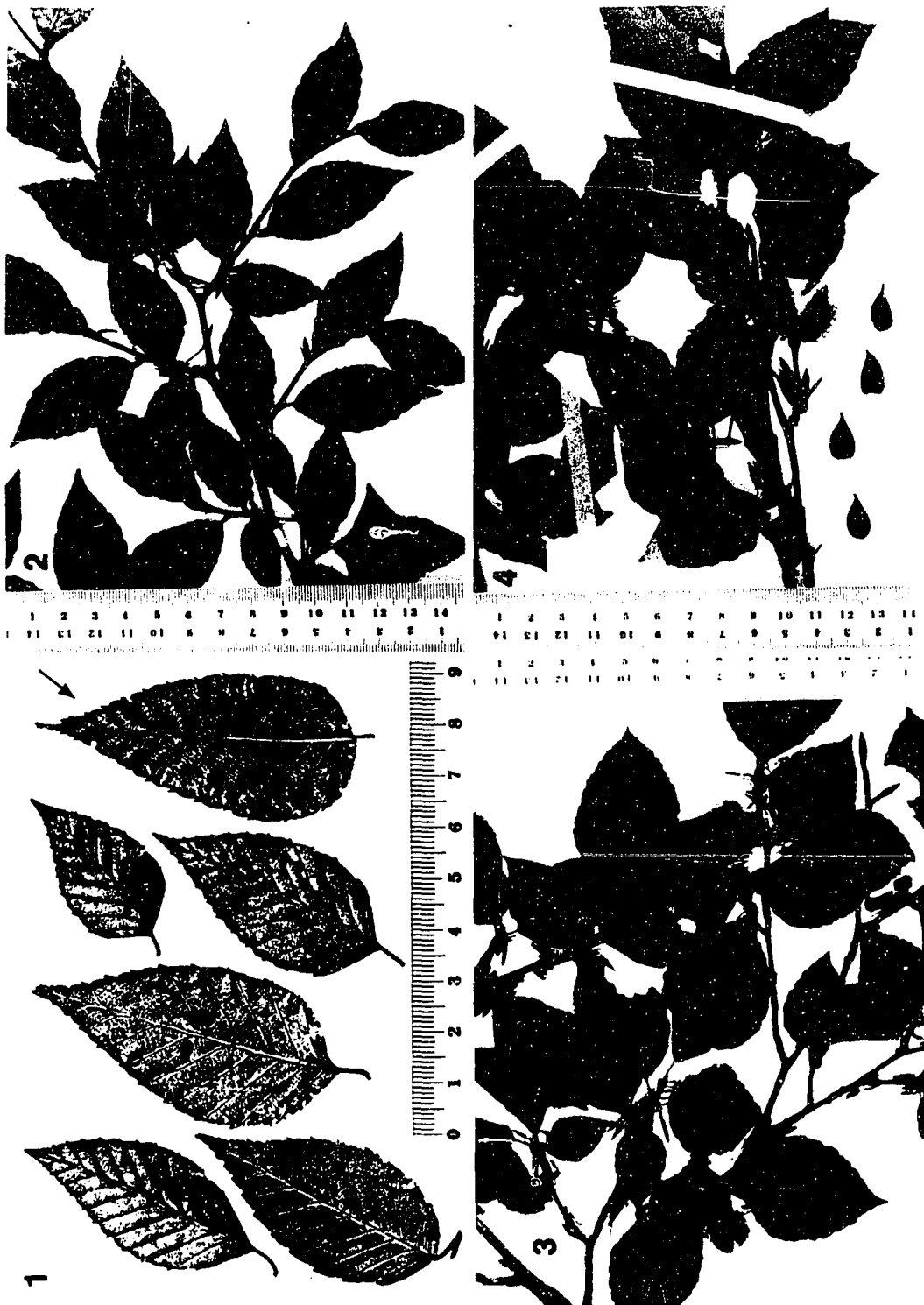


PLATE 10: F. CRENATA SUBSP. CRENATA

- 1: Kimura et al. NK-54-23-4, JAPAN-Honshu-Aomori-(Hakkodayama),
(TUS-39291). [Rather typical.]
- 2: Boufford & Shimizu 23454, JAPAN-Honshu-Nagano-Kita-azumi, 950 m,
(MICH). [Rather typical.]
- 3: M Amano 31, JAPAN-Honshu-Tokyo-Nishitama, (TUS-122258). [A
small-leaved form. Not found in N Honshu and Hokkaido.]
- 4: Collector unknown 1890-9-10, JAPAN, (ECON-1927). [Sterile. Note
the beautifully crenate margin, and the elliptic/ovate shape.
Similar leaves of even larger size are common in N Honshu.]

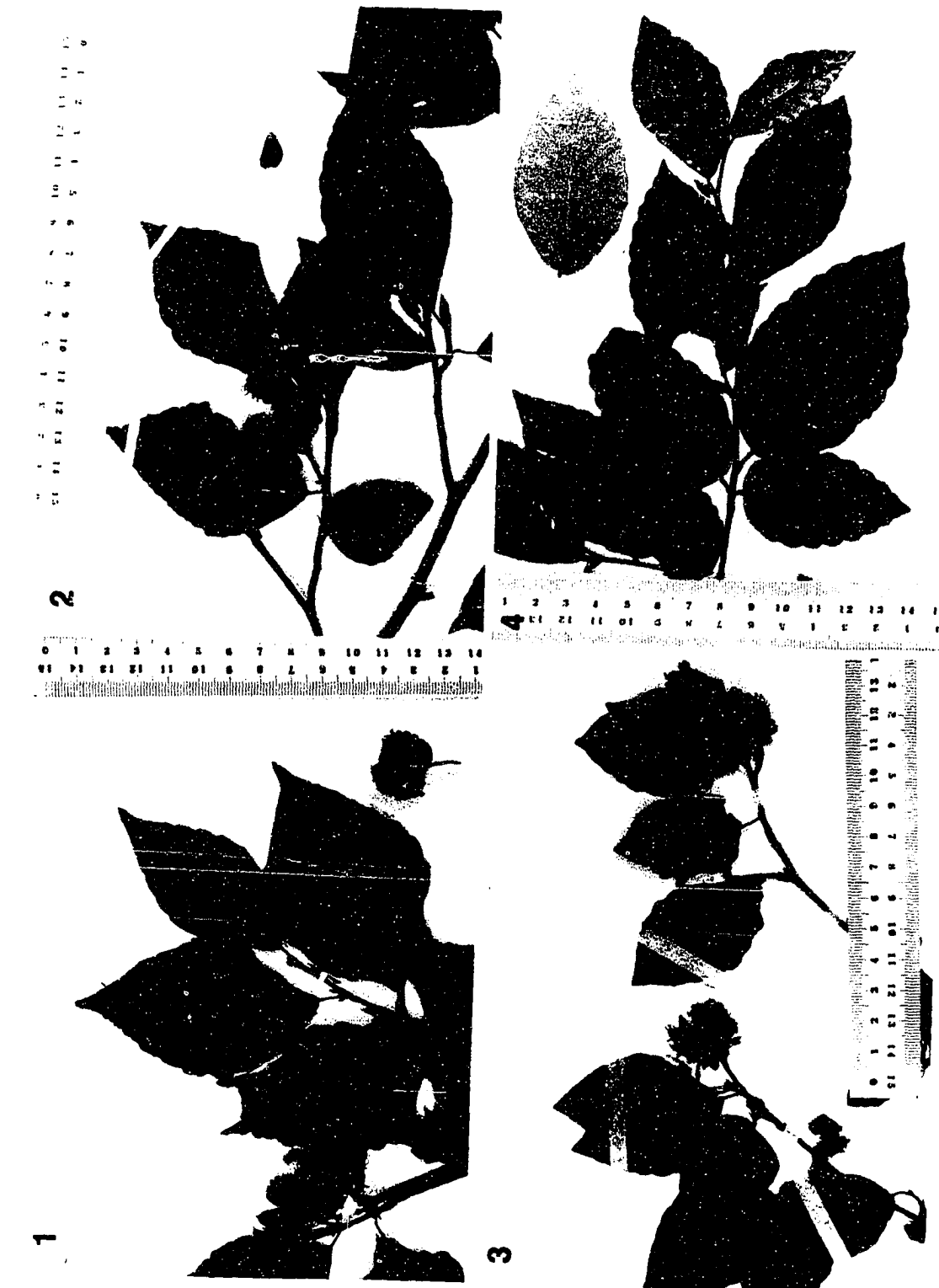


PLATE 11: F. SYLVATICA SUBSP. SYLVATICA AND F. SYLVATICA SUBSP.
ORIENTALIS

- 1: subsp. sylvatica, L Holm-Nielsen et al. 1974-8-9, GERMANY-Schleswig-Holstein, (A). [Leaves similar to some fewer-veined subsp. orientalis. except the evidently less well developed long white hairs. Compare this collection with that of subsp. orientalis shown in Fig. 3 of this plate.]
- 2: subsp. sylvatica, J Bornmueller 1931-8-0, GERMANY-Bavaria Superior, (A). [Assuming rather common expressions of gross features.]
- 3: subsp. orientalis, A Baytop 1968-6-12 (= ISTE-13288), TURKEY-A2-Kirklareli, 700 m, (E). [The leaf at the lower left corner is more representative for subsp. orientalis than others in shape. The leaf-margin of this collection is common for subsp. orientalis, but it is seldom encountered in subsp. sylvatica.]
- 4: subsp. orientalis, C Tobey 2292, TURKEY-A5/6-Samsun, 1,000 m, (E). [Rather typical.]



PLATE 12: F. SYLVATICA SUBSP. HOHENACKERIANA

- 1: T Alexeenko 84-b (1900-8-3), AZERBAJDZHAN-Baku-Kuba, (A). [Also see the following picture of leaves on sterile shoots. A biologically very typical collection, as shown in leaves on both fruiting and sterile shoots, and in cupules. Note the (slightly) subcordate very-base of leaves of both pictures.]
- 2: T Alexeenko 84-b (1900-7-21), AZERBAJDZHAN-Baku-Kuba, (G). [Sterile. Bearing the same collection number as the above one.]
- 3: RF Hohenacker s.n., CAUCASUS-(AZERBAJDZHAN-Talysh), (G). [TYPE. Typical and pure. Note the outline of the broken leaf at the left - not seen in neither of the other two subspecies.]
- 4: TS Elias 6477, RUSSIJA-Krasnodar-Novorossiisk, (NY). [Not very typical, but a good subsp. hohenackeriana in any consideration.]



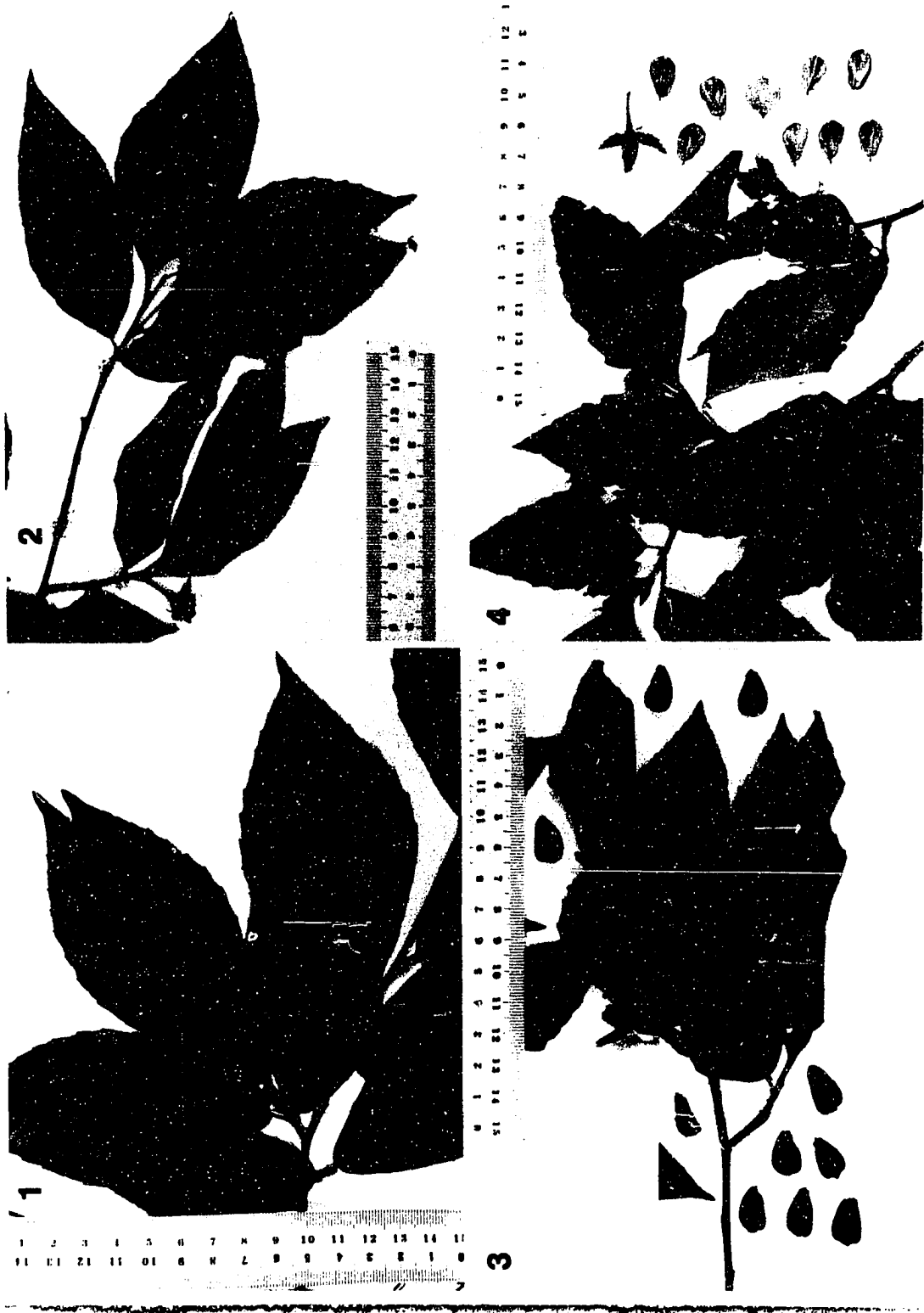
PLATE 13: F. GRANDIFOLIA SUBSP. CAROLINIANA AND F. GRANDIFOLIA SUBSP.
GRANDIFOLIA

- 1: subsp. caroliniana, RC Clark 14167, USA-Alabama-Fayette, (NCU-353946). [Rather typical. Note the oblong leaves, their slightly serrate margin, and their slightly subcordate very-base.]
- 2: subsp. caroliniana, JD Ray 6631, USA-Mississippi, (NCU-193375). [Very similar to the above collection.]
- 3: subsp. grandifolia, JH Soper 2664, CANADA-Ontario, (GH). [Rather typical. Note the rhombic shape and the sharp teeth of the leaves.]
- 4: subsp. grandifolia, ML Fernald et al. 7311, CANADA-Prince Edward Island-Queens, (GH). [Of rather common occurrence.]



PLATE 14: F. GRANDIFOLIA SUBSP. GRANDIFOLIA AND F. GRANDIFOLIA SUBSP.
MEXICANA

- 1: subsp. ?, Collector unknown 540, USA, (E). [Sterile. Very rare. Found scattered more within the northern one third of the extra-Mexican range of F. grandifolia, in which all examined fruiting collections are rather pure subsp. grandifolia. Similar to the leaves on the sterile shoots of F. sylvatica subsp. hohenackeriana at first glance, but this American collection lacks conspicuous long whitish hairs along major veins and associated with pocket-domatia - highly diagnostic for the Hohenacker's beech. Furthermore, the configuration of leaf-margin of this collection is not found in that W Eurasian beech.]
- 2: subsp. mexicana, AJ Sharp 46-169, MEXICO-Hidalgo-Tutotepec, 2,000 m, (TENN). [At anthesis. Compared with leaves on sterile shoots, these leaves are a bit smaller; with a narrower base, a slightly higher broadest-portion, and a serration less conspicuous.]
- 3: subsp. mexicana, AJ Sharp 52-106, MEXICO-Tamaulipas-Gomez Farias, (TENN). [Much thicker and smaller than leaves on sterile shoots. Also having a smaller l/w ratio than the latter. Note the strips on nut-surface.]
- 4: subsp. mexicana, H Puig 7219, MEXICO-Tamaulipas-Gomez Farias, 1,450 m, (MEXU-391209). [Not greatly different from the above collection, but bearing trullate leaves with coarse serration. Also note the strips on nut-surface - an autapomorphy of F. grandifolia.]



PLATES 15-20: CLOSE-UPS OF CUPULE/NUT COMPLEX

(Comments are restricted to the cupule/nut complex itself)

PLATE 15: SUBGENUS ENGLERIANA 1

- 1: F. japonica subsp. japonica, Y Tateishi & TT Chen 10237, JAPAN-Honshu-Fukushima-Iwase, 600-800 m, (TUS-99724). [Nuts had not attained their full size, judging from the common situation of this taxon.]
- 2: F. japonica subsp. japonica, J Bisset 4256, JAPAN-Honshu-Tochigi-Nikko, (E). [Cupule-appendages much reduced, compared with the normal cupules seen in this taxon. Note the two angle-like protuberances just below the cupule-valves. They are the positions of the two scars left by two subtending bracts of the cupule - the only residual structure of a much reduced female inflorescence.]
- 3: F. engleriana, Elsik & Erwin 1957, cult. in (A), AA-383-27-A, graft from AA-7416, from CHINA-Hubei, (A). [Note the same two projections. A Rather typical cupule/nut complex for this taxon. Also note the distal wing-like extensions on the nuts, and some forked cupule-appendages. The upper side of the nut-wings of this taxon is normally perpendicular to the longitudinal axis of the nut, just as is shown here.]
- 4: F. engleriana, Elsik et al. 253, cult. in (A), AA-7416-A, from CHINA-Hubei, (A). [At anthesis. From an individual of the same genetic composition as the individual that has produced a mature cupule/nut complex shown in the immediately above figure.]



PLATE 16: SUBGENUS ENGLERIANA 2

- 1: F. okamotoi, S Noshiro 1606, JAPAN-Honshu-Yamanashi-Enzan, (TUS-75454). [TYPE.]
- 2: F. japonica subsp. angustifolia, Michener & Bennett 1974, cult. in (A), AA-23182-A, source unknown, (A). [TYPE. Note the two projections very prominently seen in the subgenus. Also note the peculiar-shaped wings close to the apex of nut-angles.]
- 3: F. japonica subsp. angustifolia, Elsik & Whitaker 1970, cult. in (A), AA-14587-B, from JAPAN, (A). [Note the two projections discussed above.]
- 4: F. japonica subsp. angustifolia, PS Green 1964-10-8, cult. in (A), AA-14587-B, from JAPAN, (A). [From the same tree that had produced in an earlier year a cupule/nut complex shown in the immediately above figure. Very similar to the one shown in the Fig. 2 of this plate (from the type collection), except the 7-valved configuration of this cupule. All other cupules present on this sheet are 4-valved.]

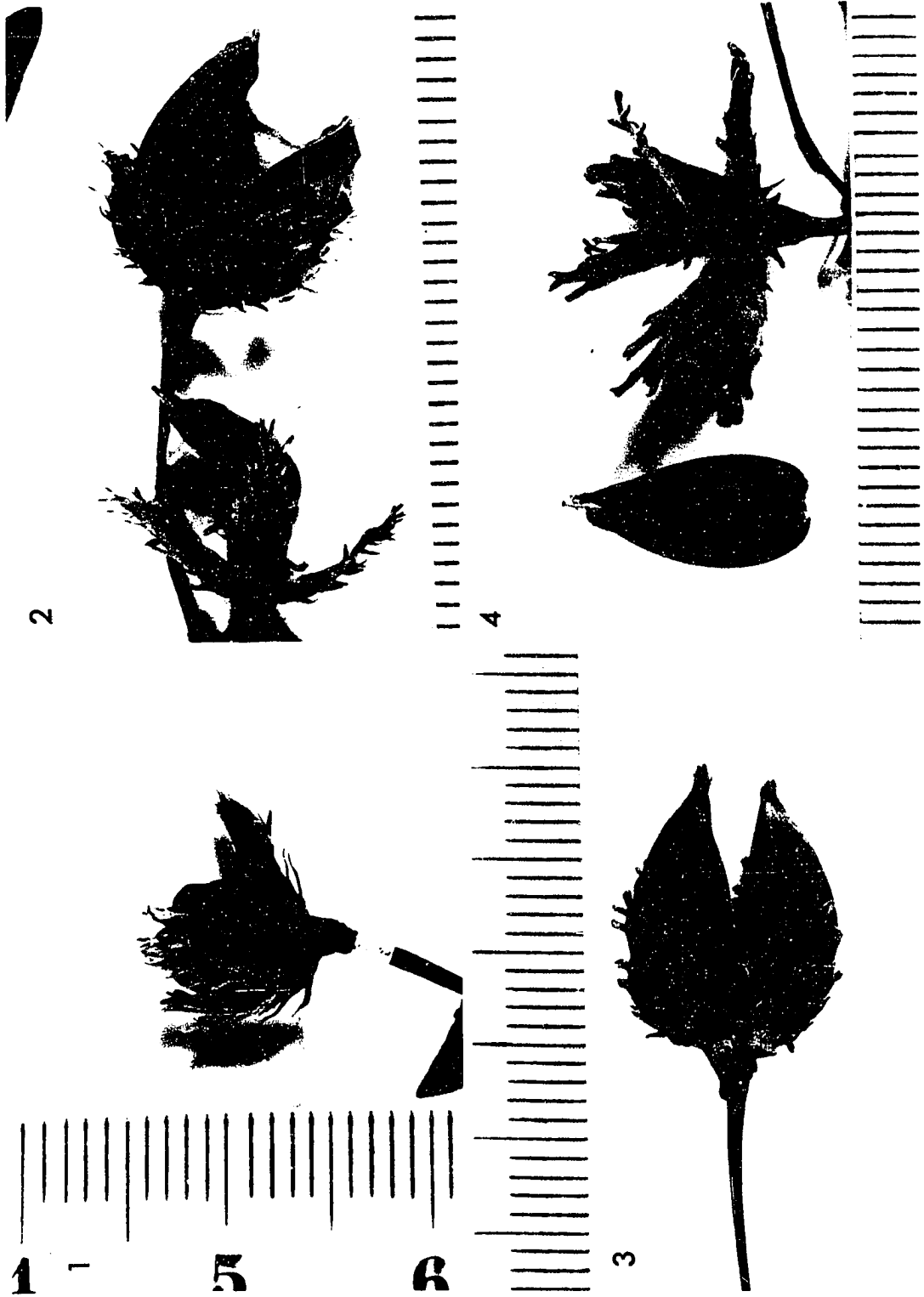


PLATE 17: SUBGENUS FAGUS, SECTION LONGIPETIOLATA

- 1: F. longipetiolata, A Henry 5334-A, CHINA-Hubei-Jiensi, (US).
[TYPE. Biologically typical cupule/nut complex.]
- 2: F. longipetiolata, YW Taam 738, CHINA-Guangdong-Xinfeng-Chaping,
(A). [Rather typical.]
- 3: F. bijiensis, PH Yu 766, CHINA-Gueizhou-Bijie, 1,450 m, (IBSC-
343516). [TYPE. Shape of nuts is similar to that of F. lucida.]
- 4: F. tientaiensis, LH Lou 6064, CHINA-Zhejiang-Tientai-
(Huadingshan), 500 m, type-tree, (ZJFC). [Rather similar to the
Zhejiang population(s) of F. hayatae subsp. pashanica, if
properly reduced in size.]

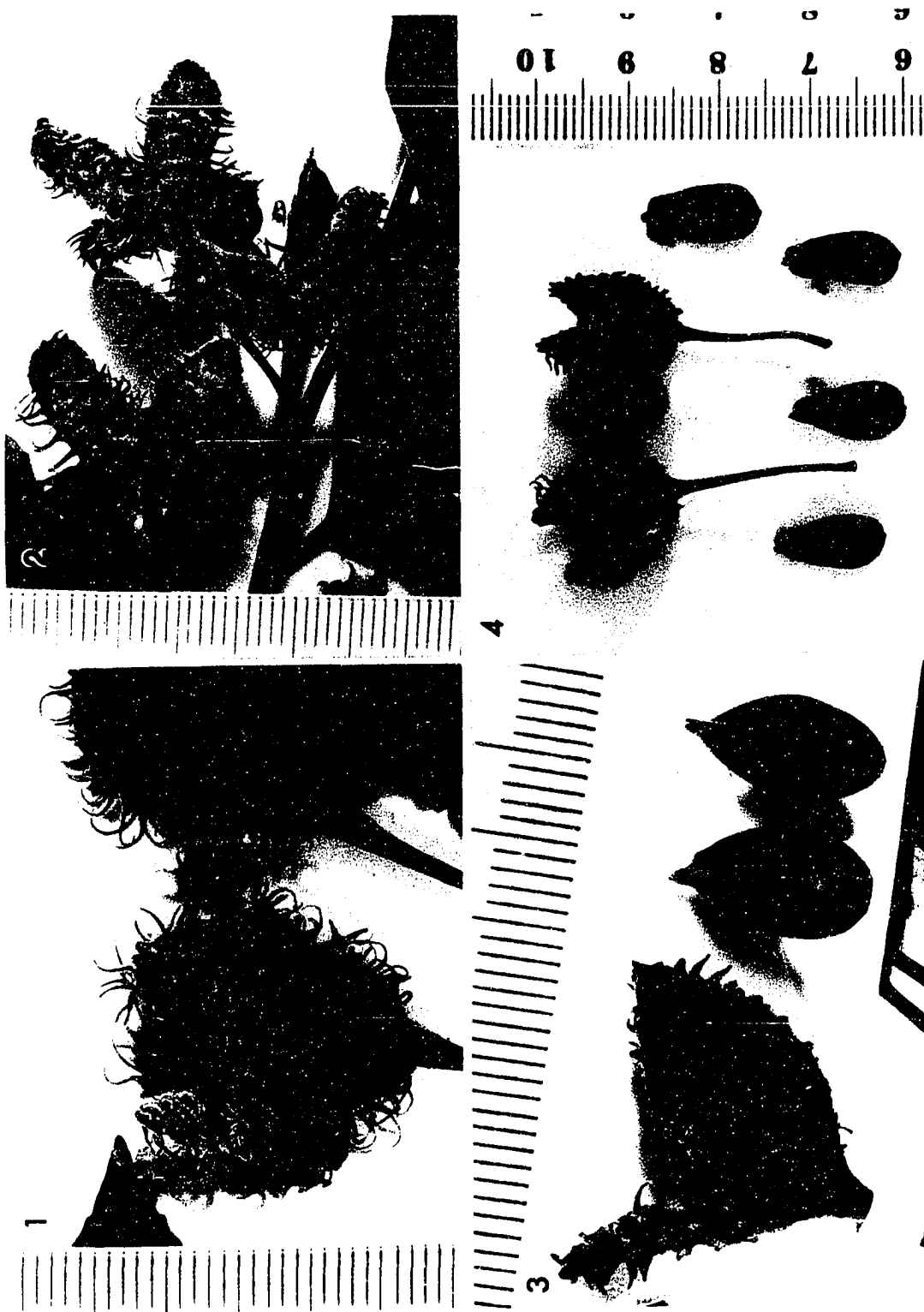


PLATE 18: SUBGENUS FAGUS, SECTION LUCIDA

- 1: F. lucida, Sino-Am 1980 W Hubei Exp. 1479, CHINA-Hubei-Shennongjia, 2,000 m, (NY). [Tips of the cupule-valves are damaged by rodents. A very atypical cupule and peduncle. Three-valved cupules are normal for this taxon, but the appendages of this collection are too peculiar in their much reduced situation. An abraded fossil cupule of this kind would perhaps be described as without appendages. The peduncle of this cupule is too long for a cupule of F. lucida of similar size. This collection is the only collection of F. lucida (# 1479, 2,000 m) available to me from Shennongjia of W Hubei, collected by the Sino-Am 1980 W Hubei Expedition. This team also collected F. engleriana (# 1221, 1,780 m; # 1309, 2,000 m) and F. hayatae subsp. pashanica (# 1485, 2,050 m).]
- 2: F. chienii, WC Cheng 2903, CHINA-Sichuan-Pingwu, 1,300 m, (E, G). [TYPE. Note the evidently winged nut-angles.]
- 3: F. crenata subsp. crenata, Kimura et al. NK-54-23-4, JAPAN-Honshu-Aomori-(Hakkodayama), (TUS-39291). [Rather common.]
- 4: F. crenata subsp. undulata, M Furuse 1952-6-13 (= Exsiccata NSM-539), JAPAN-Honshu-Shizuoka-Ashitakayama, (A). [Rather common.]



PLATE 19: SUBGENUS FAGUS, SECTIONS LUCIDA AND FAGUS

- 1: F. hayatae subsp. pashanica, Sino-Am 1980 W Hubei Exp. 1485, CHINA-Hubei-Shennongjia, 2,050 m, 4 m tall, (A). [Typical for this subspecies, though the peduncle is close to one end of the range - shorter and stouter. Subspecies hayatae has shorter and stouter peduncle than subsp. pashanica, otherwise the two are indistinguishable in cupule/nut complex.]
- 2: F. sylvatica subsp. sylvatica, J Bornmueller 1931-8-0, GERMANY-Bavaria Superior, (A). [Rather common, though the density of appendages is a bit lower even abrasion is evident for the right one. Note the few linear appendages very close to the base of cupule-valves. They are more easily abraded off than the (thin) thread-like ones, due to their weaker and smaller attaching area.]
- 3: F. sylvatica subsp. orientalis, A Baytop 1968-6-12 (=ISTE-13288), TURKEY-A2-Kirklareli, 700 m, (E). [Typical.]
- 4: F. sylvatica subsp. hohenackeriana, TS Elias 3133, ARMENIA-Haghartsin, 1,800-1,900 m, (NY). [Typical. Note the linear basally-borne appendages. Also note the prominently winged nuts of the three representative collections of the three subspecies of F. sylvatica shown here.]

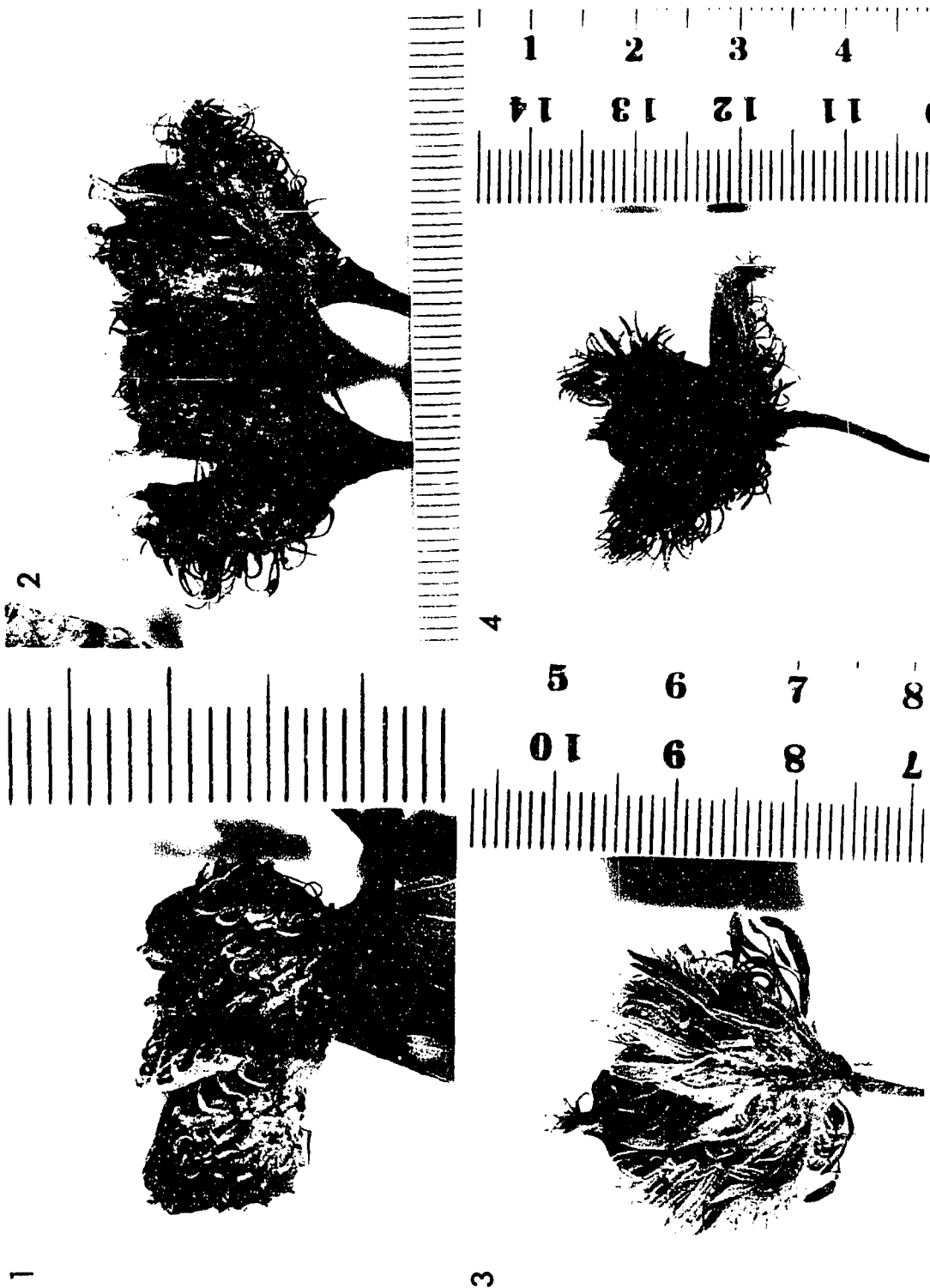
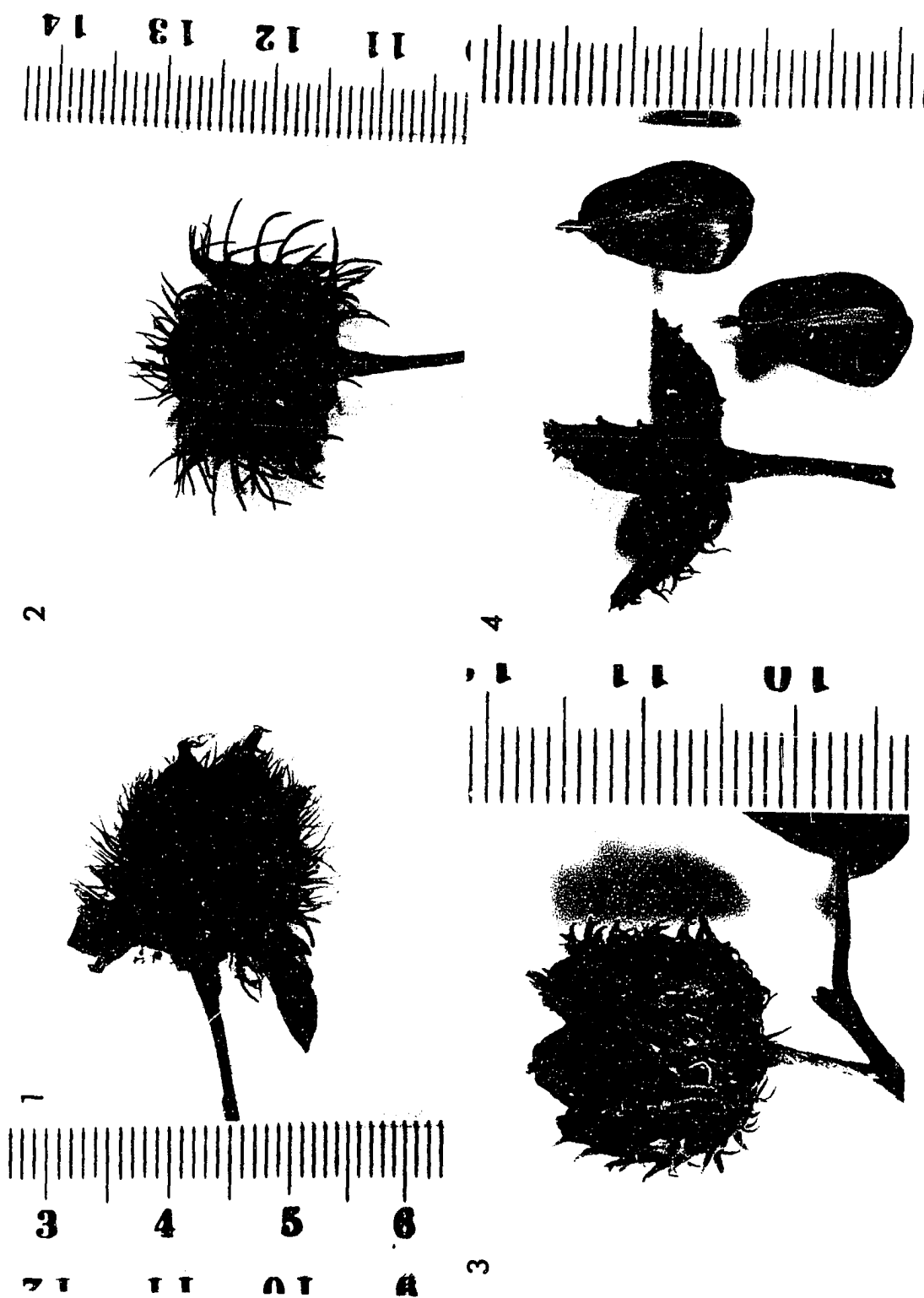


PLATE 20: SUBGENUS FAGUS, SECTION GRANDIFOLIA (F. GRANDIFOLIA)

- 1: subsp. grandifolia, FC Gates 11859, USA-Michigan-Cheboygan-Wolff Bog, (A). [Typical except the spathulate-foliaceous appendages at the base of cupule. Populations producing spathulate-foliaceous basally-borne appendages are not very rare well within the range of subsp. grandifolia.]
- 2: subsp. grandifolia, a scattered cupule/nut complex in a specimen folder. [Of a sort not rare within the range of subsp. grandifolia, but never found in the range of subsp. caroliniana. The leaves of these populations (individuals) are closer to those typical for subsp. grandifolia. Some of the similarities and differences between this and the other two pictured cupules of extra-Mexican F. grandifolia in the gross features of cupule-valve and cupule-appendages can be observed on the figures. For this cupule, also note that a few basal appendages are linear, and that some lower appendages show a tendency to become linear.]
- 3: subsp. caroliniana, RC Clark 14167, USA-Alabama-Fayette, (NCU-353946). [Typical. Note the few forked appendages. Also note the few short linear-like appendages at the base of cupule-valves. Clearly linear basally-borne appendages are, however, not very rare well within the range (both geographic and ecological) of subsp. caroliniana.]
- 4: subsp. mexicana, H Puig 7219, MEXICO-Tamaulipas-Gomez Farias, 1,450 m, (MEXU-391209). [Typical. Many appendages are broken. Note the two residual (unabraded) basally-borne short linear

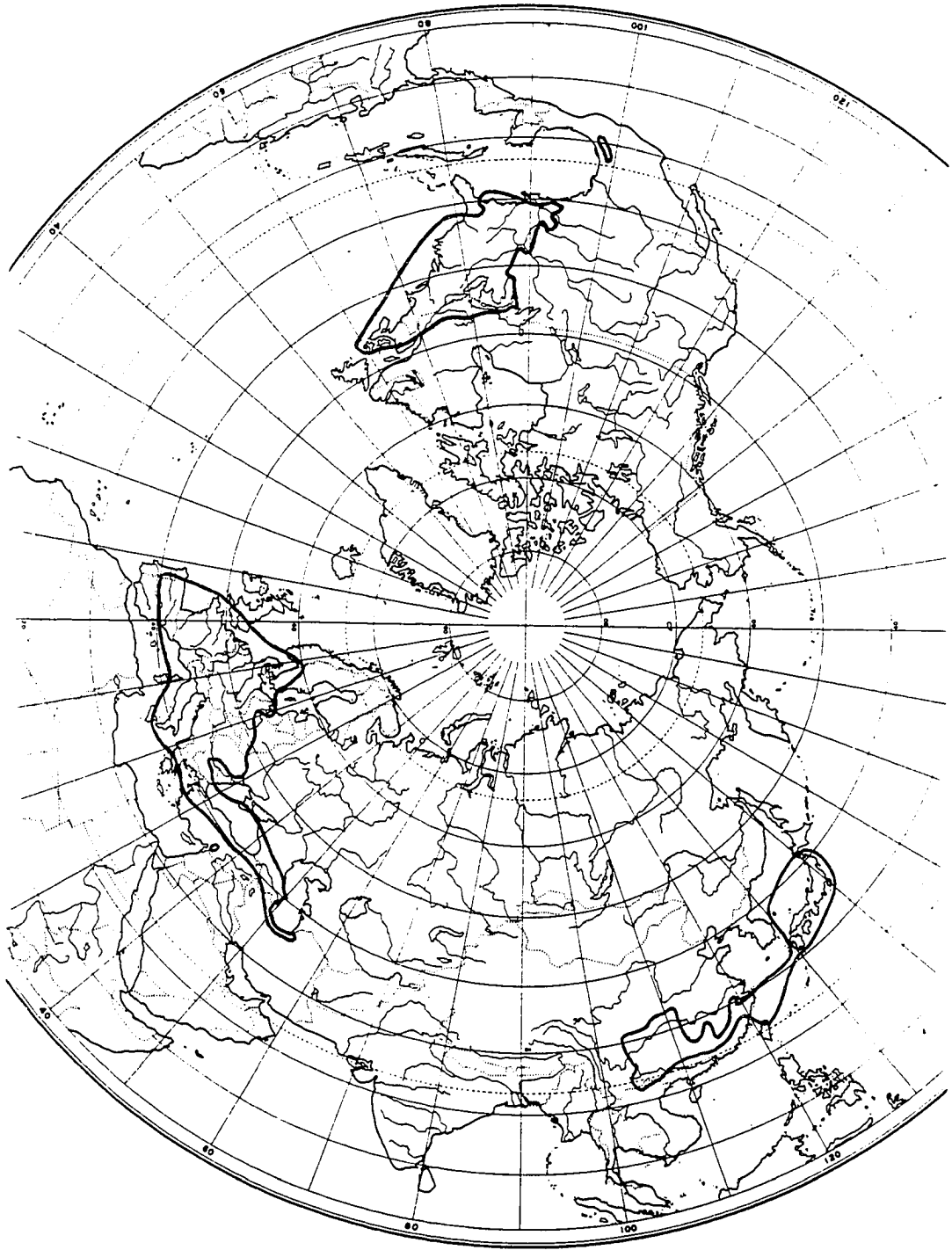
appendages. Also note the prominent nut-wings and the striped nut-surface - both are typical for F. grandifolia.]



APPENDIX 4

DISTRIBUTION MAPS

MAP 1: DISTRIBUTION OF THE GENUS FAGUS TOURN. EX L.

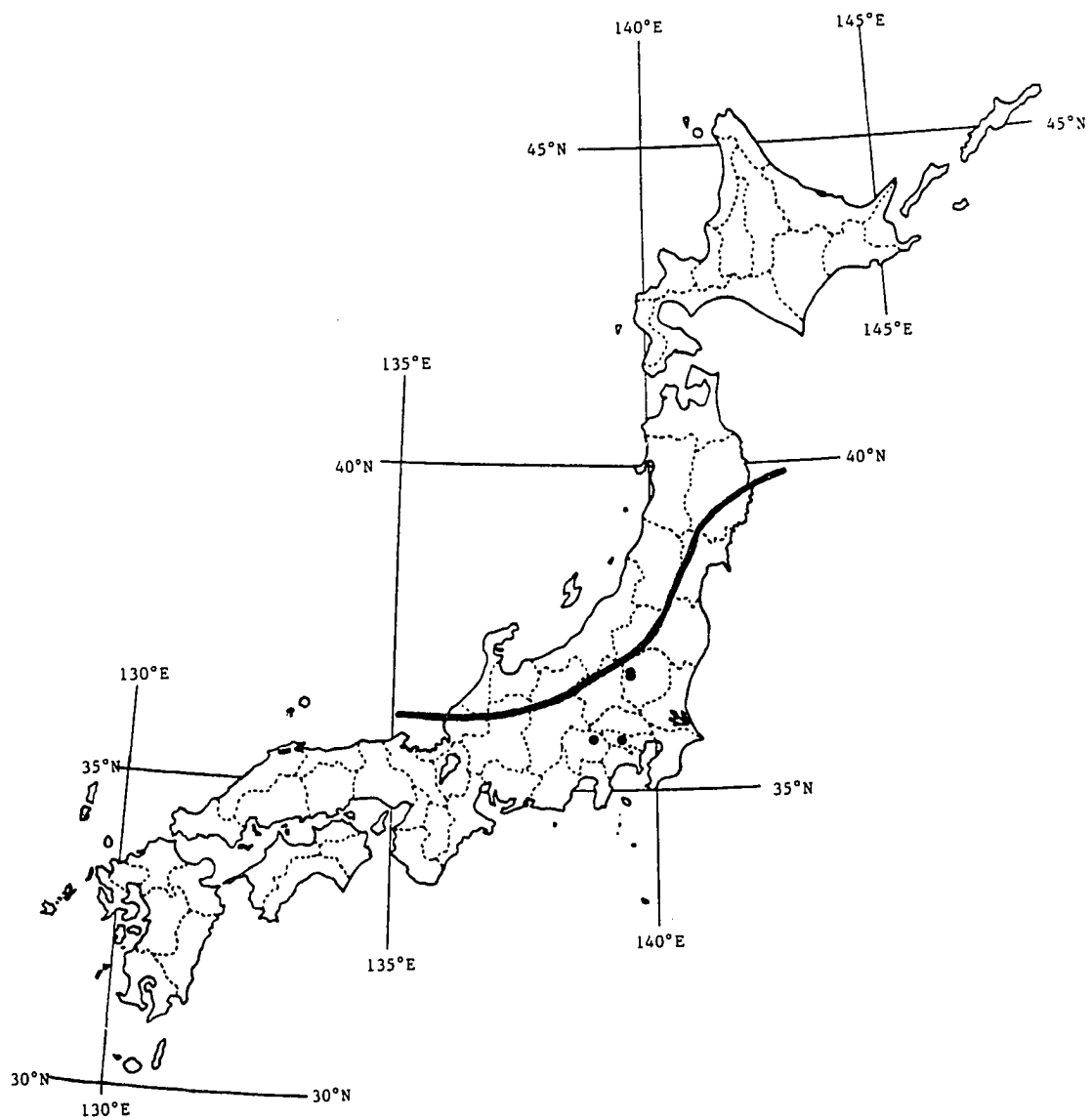


MAP 2: DISTRIBUTION OF F. JAPONICA AND F. OKAMOTOI

F. JAPONICA SUBSP. JAPONICA: South of the thick and sinuous line crossing central Honshu.

F. JAPONICA SUBSP. ANGUSTIFOLIA: Unknown, because the known collections are all from cultivated individuals. Nevertheless, its geographic range in Japan is not expected to be outside of that of subsp. japonica.

F. OKAMOTOI: Dots. Four in total, so far as I know.



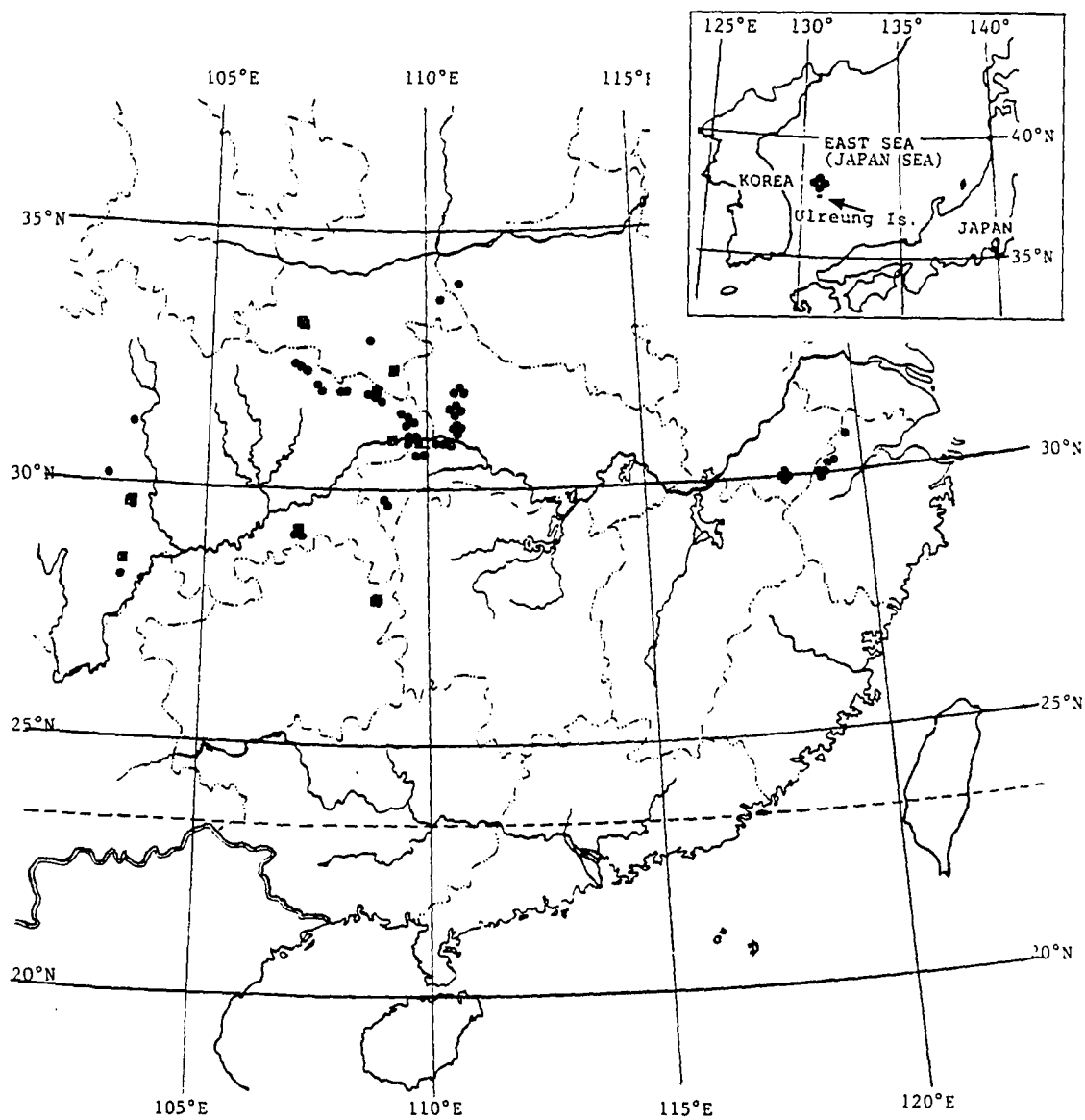
MAP 3: DISTRIBUTION OF F. ENGLERIANA

Dots are based on the collections examined by me.

Squares are selected from the collection-citation list provided in Chang (1966). This taxon is unmistakable in China among the Chinese beeches.

NOTE:

If more than four collections are from the same locality or from a very small region in consideration of such a small-scaled base-map, I only drop four spots in a cluster (not a chain). Generally speaking, such a cluster may be regarded as representing an abundant occurrence of this taxon.



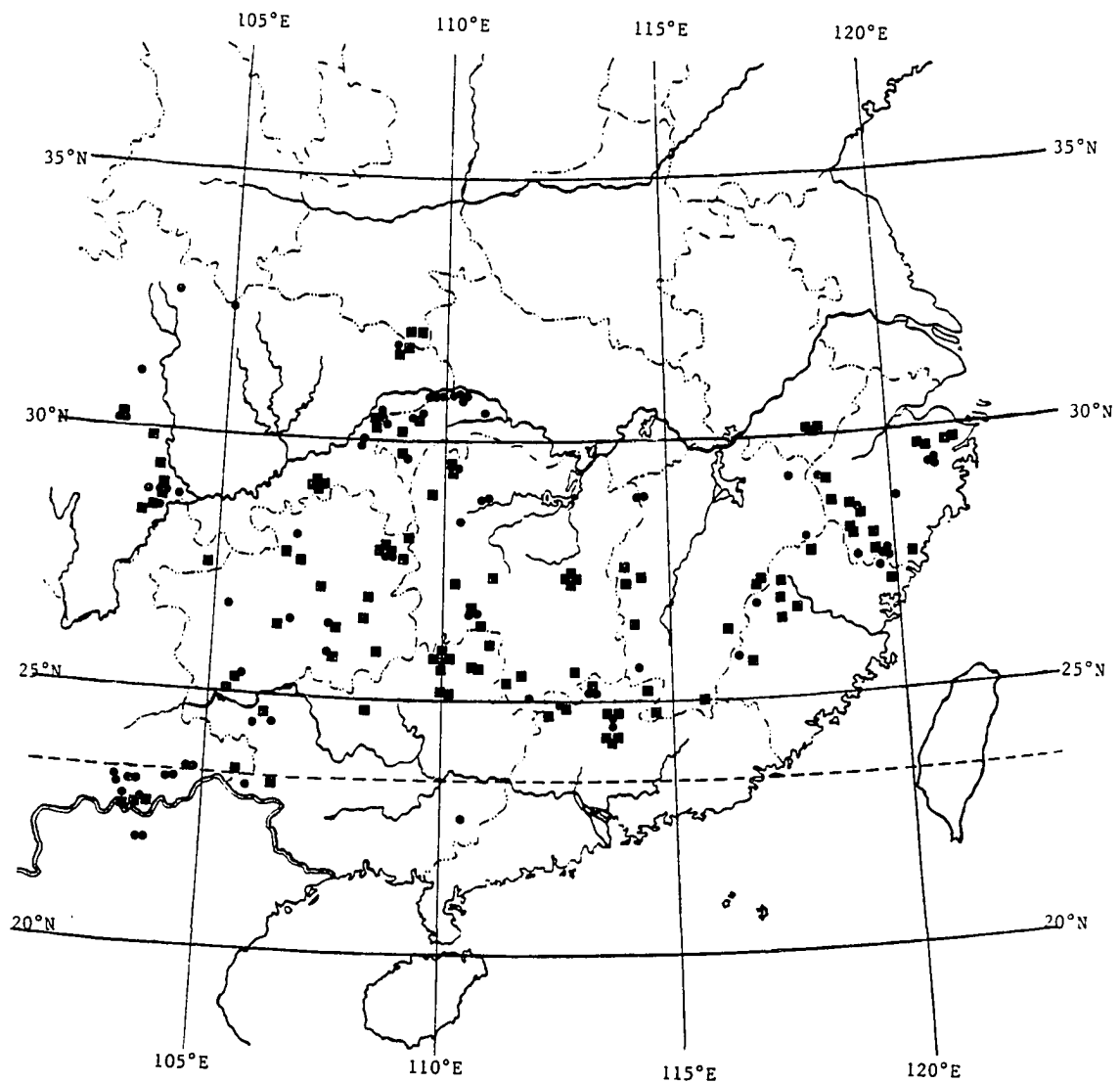
MAP 4: DISTRIBUTION OF F. LONGIPETIOLATA

Dots refer to the collections at my disposal.

Squares refer to the collections cited by Chang in his 1966 revision of the Chinese beeches but not represented in the collections at my hand. I trust his identifications on this taxon.

NOTE:

The meaning of a four-spotted cluster on this map is the same as that on the previous map.



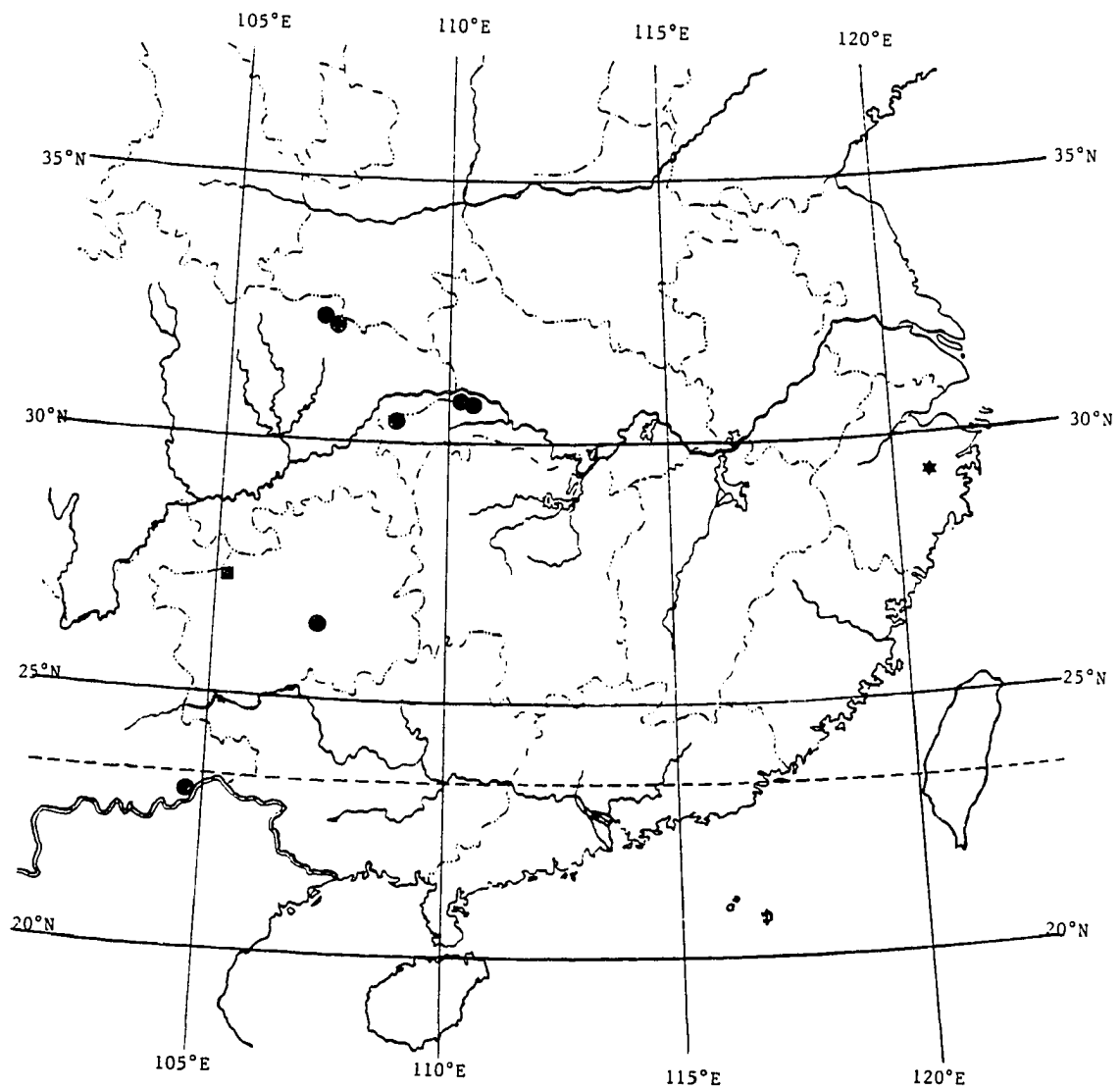
MAP 5: DISTRIBUTION OF F. BREVIPETIOLATA, F. BIJIENSIS, AND

F. TIENTAIENSIS

F. BREVIPETIOLATA: Dots.

F. BIJIENSIS: A single square, representing the type collection.

F. TIENTAIENSIS: A single star, representing the type-tree (two collections).



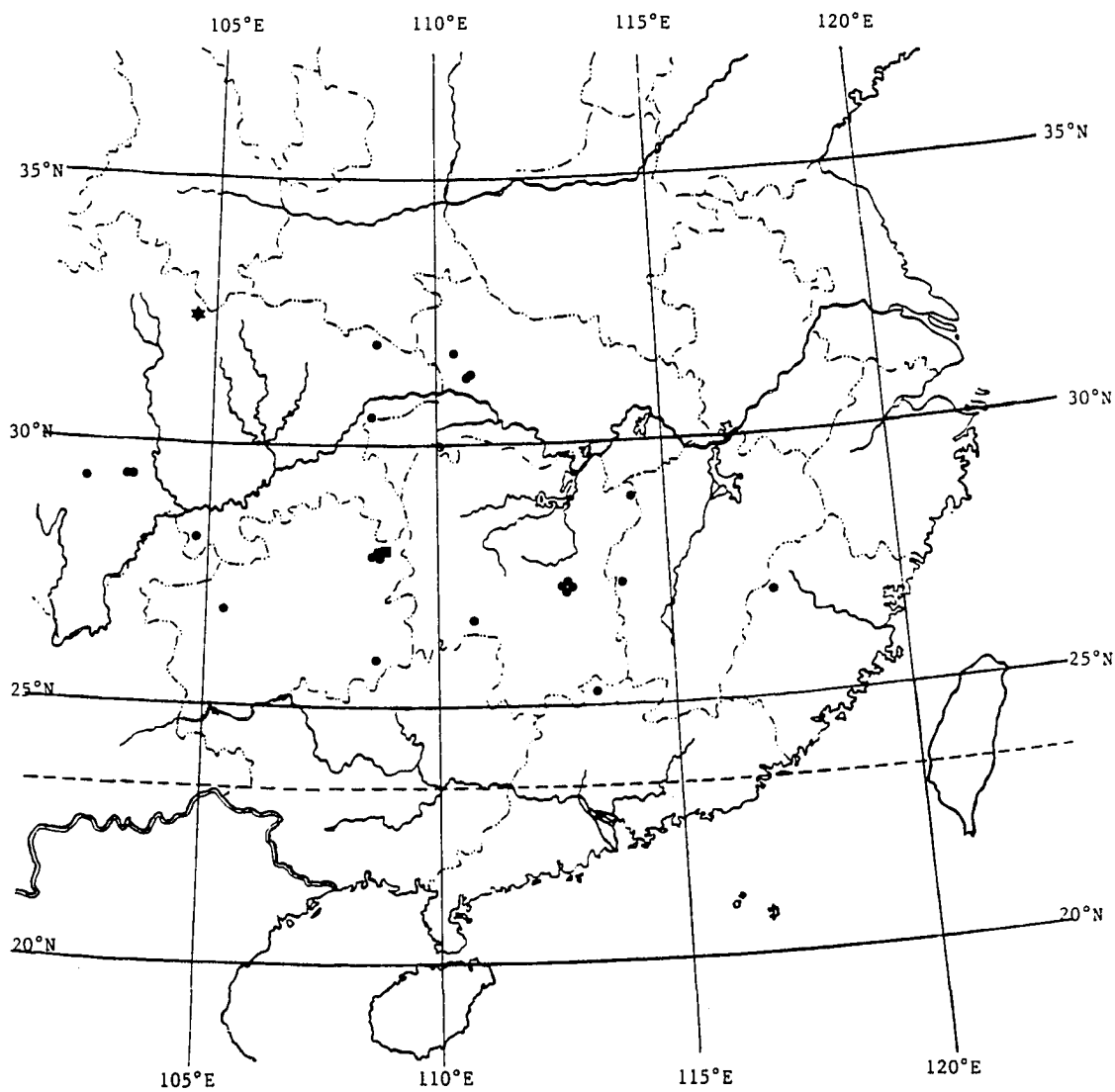
MAP 6: DISTRIBUTION OF F. LUCIDA AND F. CHIENII

F. LUCIDA: Dots. The single square added in refers to several other collections cited in Chang (1966), from a montane region - Fanjingshan where F. hayatae subsp. pashanica has not been reported by previous authors, and is not represented in the collections at my disposal.

F. CHIENII: A single star, referring to the type collection.

NOTE:

Again, the meaning of a four-spotted cluster bears the same meaning as before.



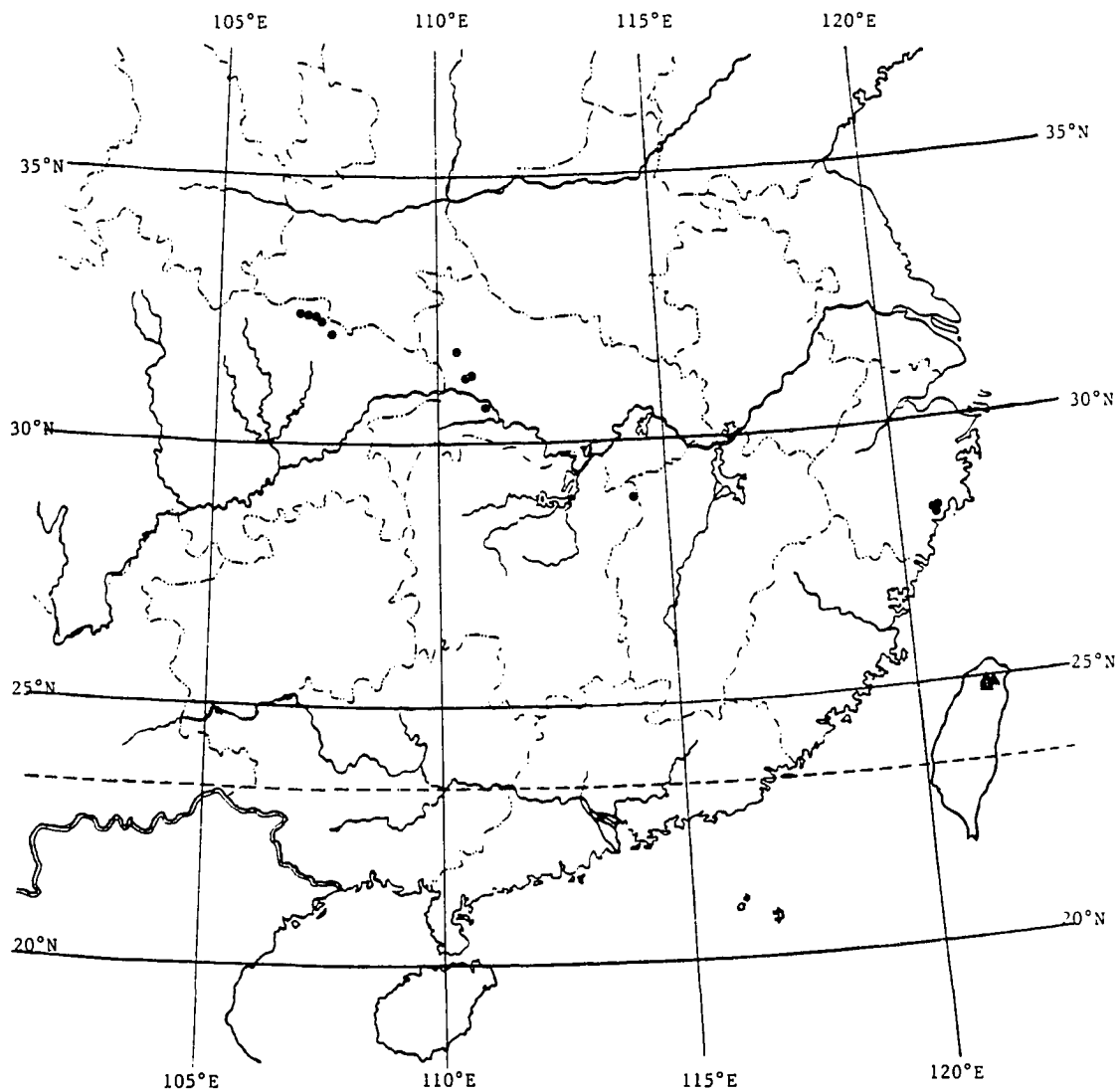
MAP 7: DISTRIBUTION OF F. HAYATAE

SUBSP. HAYATAE: Triangles.

SUBSP. PASHANICA: Dots.

NOTE:

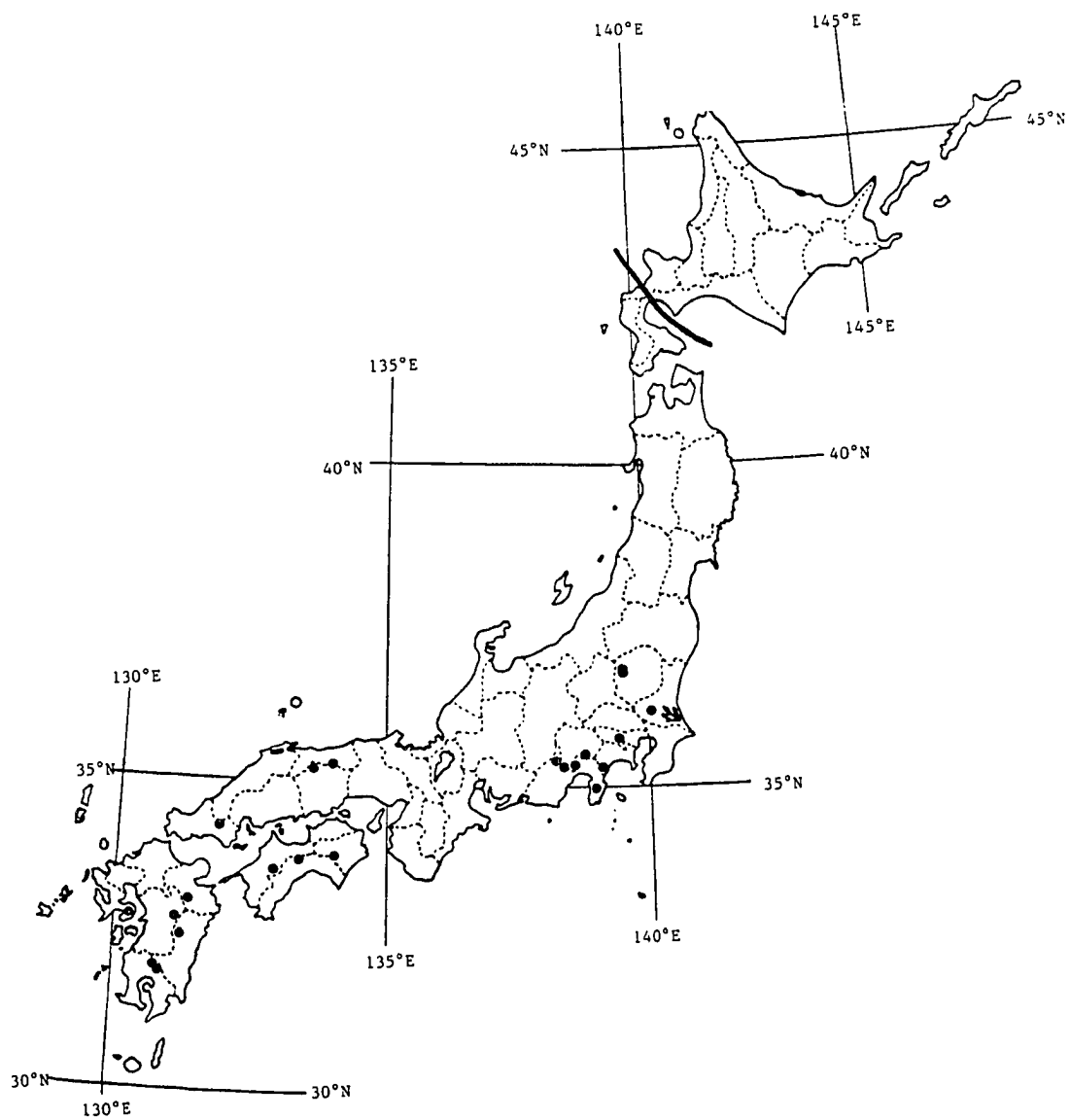
A three-spotted chain or cluster refers to an abundant occurrence.



MAP 8: DISTRIBUTION OF F. CRENATA

SUBSP. CRENATA: South of the thick line crossing southern Hokkaido.

SUBSP. UNDULATA: Dots. Within an imaginary closed sinuous line encircling all these dots, however, I am not very sure about the real absence of taxonomically good populations of subsp. crenata.



MAP 9: DISTRIBUTION OF F. SYLVATICA

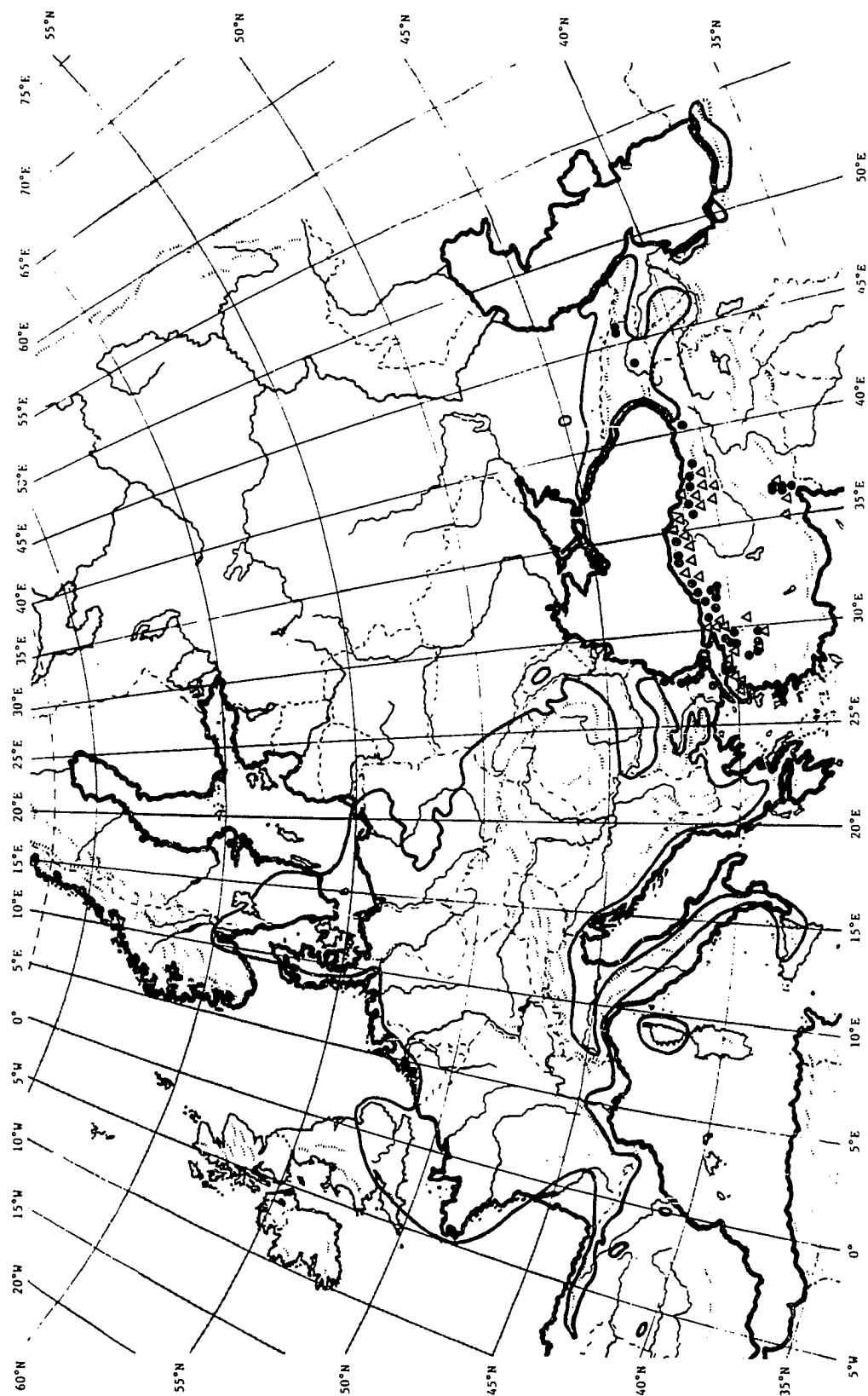
SUBSP. SYLVATICA: Sinuous closed lines west of 30 or 35 degrees E. See the note below.

SUBSP. ORIENTALIS: Dots refer to the collections examined by me. Hollow triangles are selected Turkish collections cited by Browicz (1982) and Yaltirik (1982), from the region in which all collections examined by me are good subsp. orientalis in my concept.

SUBSP. HOHENACKERIANA: Sinuous closed lines east of 30 or 35 degrees E. See the note below.

NOTE:

Beech populations in Krym (Crimea) of Ukraine are really taxonomically abominable. In total, they may represent a genetically "mixed" population-group among all of the three subspecies of F. sylvatica as defined here. And it seems that the heredities of subsp. sylvatica and subsp. orientalis are better represented than that of subsp. hohenackeriana. Until some chemical or molecular markers can offer a more satisfactory solution to this issue, I am reluctant to argue strongly the taxonomic assignment of the Krym beech (= F. taurica) to either subspecies.



MAP 10: DISTRIBUTION OF F. GRANDIFOLIA

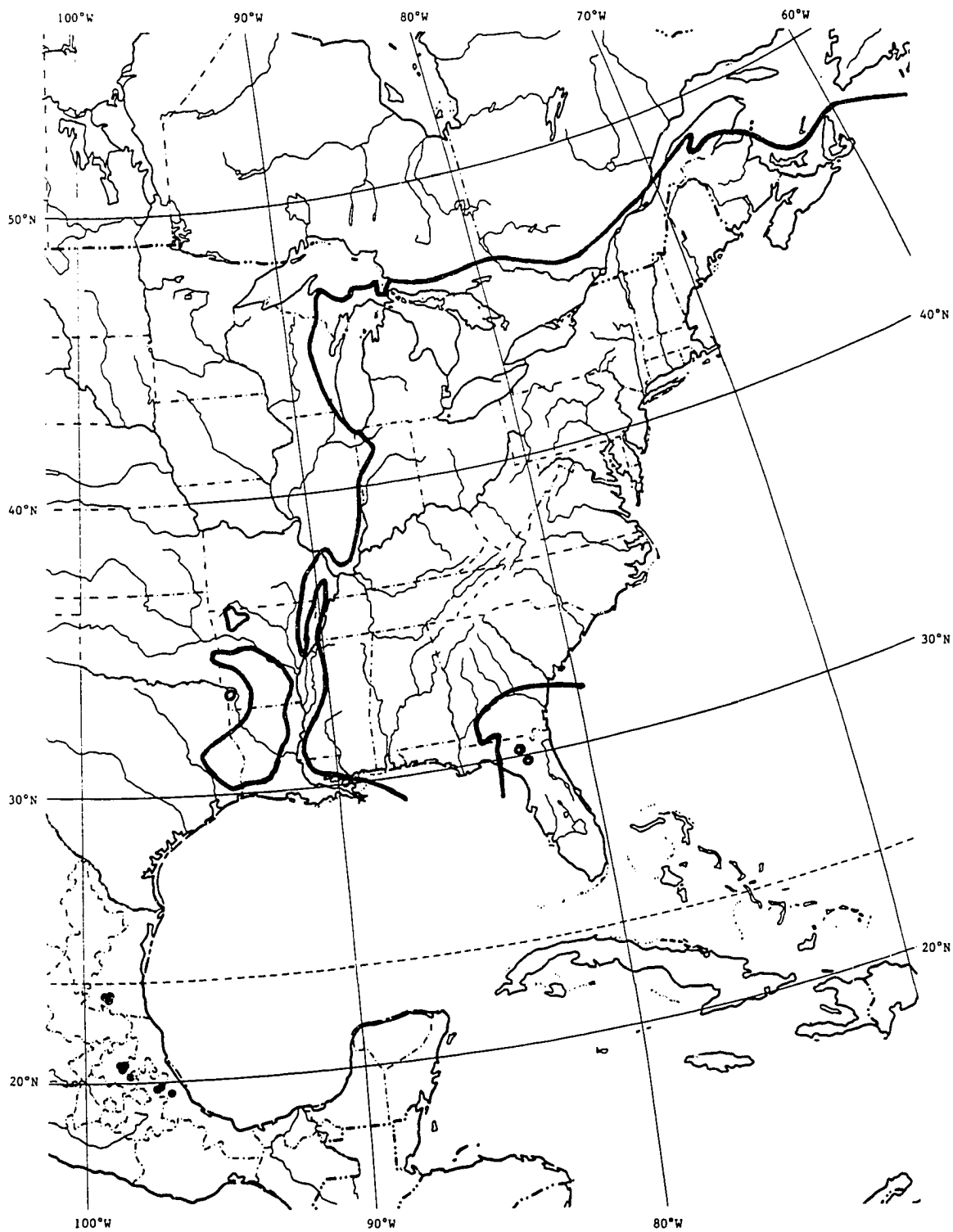
SUBSP. GRANDIFOLIA: The northern one third of the extra-Mexican range of the species, but with its southernmost range at high elevations of southern Appalachians in North Carolina and Tennessee. See the note below.

SUBSP. CAROLINIANA: The southern one third of the extra-Mexican range of the species. See the note below.

SUBSP. MEXICANA: Dots in Mexico. Three-dotted clusters refer to an abundant local occurrence.

NOTE:

The middle one third of the extra-Mexican range of F. grandifolia is populated by various intermediate populations.



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