China's Beech Forests in the Pre-Quaternary

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With 1 plate and 7 figures

Abstract

Fagus in China is never dominant in Late Cretaceous and Tertiary floras although it might reach its highest diversity in the Miocene. The genus *Fagus* was more widely distributed during the Palaeogene than in the Neogene. Furthermore, the ecological requirements of *Fagus* in the Palaeogene seem much broader than those in the Neogene onwards. This is because the Palaeogene floras containing *Fagus* lived in various conditions from an arid and hot climate to a humid and warm habitat. Additionally, *Fagus* then coexisted with many kinds of hygrophilous, thermophilous and xerophilous plants. However, the wide distribution, broad ecological adaptation and species composition changed greatly in the Neogene. The Neogene *Fagus*-containing floras are slightly more similar to the modern beech forests than the Palaeogene ones, although a big difference remains. Chinese fossil data document the post-Tertiary development of the modern beech forests.

Key words: China, *Fagus*, forest change, mega-/microfossils, pre-Quaternary

Introduction

Fagus (beech) is one of the most important trees in the temperate and subtropical forests of the Northern Hemisphere (Peters 1997). There are eleven species in total, seven occur in China. The Chinese species are of significance because their occurrence is restricted to the montane region of south China where they associate with numerous evergreen trees (Chang & Huang 1988, Zhou & Li 1994; Cao et al. 1995; Peters 1997). Moreover, it is believed that these species are so sensitive to heat and water conditions that they do not occur in lowland area of China (Hong & An 1993; Cao et al. 1995).

An attempt has been made to explain the pre-Quaternary development of *Fagus* forests in China (Zhou & Li 1994; Peters 1997). However, these studies are mostly based on incomplete literature data including many errors. In the present paper, all the fossil data of *Fagus* from China are applied after a careful review (Liu et al. 1996; Leng 1997; Wang Wei-Ming unpublished data) to analyse the development of *Fagus* forests in the pre-Quaternary of China. The main objective is to understand the evolutionary history of beeches from floristic and ecological points of view.

Methods

There is one living beech endemic to Taiwan (see Table 1). As little information on the fossil records of *Fagus* is available, our discussion will concentrate on continental China.

Identification of fossil leaves and pollen grains belonging to the genus *Fagus* is not always easy. Furthermore, it is probably even more difficult to establish the interspecific relationships of fossil and living taxa because of the high variation in leaf morphology within the genus (Shen 1992; Liu & Momohara submitted). In order to find useful criteria to classify fossil leaves into the natural groups of *Fagus*, many palaeobotanists have tried to find characters for distinguishing infrageneric taxa, such as the number of secondary veins, leaf index and foliar cuticles (Tanai 1974; Zetter 1984; Kvacek & Walther 1991). Foliar macrocharacters may not be as valuable as has been claimed, although they are easily observed (Liu & Momohara submitted). Leaf cuti-

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cies are ideal to be applied in the classification of fossil beeches but they are by no means always preserved. Fossil leaves attributed to *Fagus* in China are largely preserved as impressions (Liu et al. 1996). A recent discovery of some beech leaves in the Miocene of northeast China did yield carbonized material but only the upper cuticle has been obtained (Leng 1997). Therefore, this does not provide much help to figure out the relationships between the fossil and living beeches in China. Therefore, fossil organ-species of beeches with little evolutionary significance are used in the paper (Liu et al. 1996; Leng 1997). On the other hand, unlike the pollen of *Nothofagus*, the pollen morphology in *Fagus* does not seem to provide features useful for safe identification of all species (Praglowski 1982).

Most *Fagus* fossils are recovered from terrestrial sediments. The dating is certainly sometimes controversial. In the present paper, we follow Zhang (1993, 1995) for the Late Cretaceous and Palaeogene palynofloras respectively, Liu (1988) and Wang (1992) for the Neogene palynofloras and Liu et al (1996) for the Cenozoic megafloras.

Recent beech forests in China

Seven species (including 1 variety) endemic to China have been so far documented (Chang & Huang 1988; Anonymous 1992). They are unique not only systematically but geographically and ecologically as well (Zhou & Li 1994; Cao et al. 1995; Liu & Momohara submitted).

1. Distribution: The Chinese *Fagus* species are restricted to the subtropical montane region in south China, appearing mainly between 700 m and 2500 m above sea level. They only occur as components in vertical vegetation zones between south of ca. 34 °N and north of ca. 22 °N (Fig. 1; Table 1). In a vertical zonation, they are found close to the upper limit of evergreen broadleaved forests or sometimes in a the transitional vegetation type extending into deciduous broadleaved forests. It is interesting to note that they do not occur in any horizontal vegetation zone in the same region. This is very different from their distribution pattern in Europe, Japan and North America where beeches mainly occur in the temperate deciduous forest region of both lowland and montane areas.

The distribution of each Chinese beech species is shown in Table 1.

2. Ecological requirements: Cao et al. (1995) presented a full and detailed survey of the ecological conditions of *Fagus* in China, and concluded that all the Chinese beeches require similar water and heat conditions. For Chinese beeches habitats with an annual precipitation of 740–3500 mm and a mean annual temperature ranging from 5 to 17 °C are optimal (Table 2). Table 2 shows the basic differences between the Chinese beeches and the others in a simple way. The habitats in China's beech forests are more humid than those in lowland Europe and North America (Cao et al. 1995).

Table 1

Geographical ranges of *Fagus* in China and the forest types in which they live (based on Xu et al. 1985; Chang & Huang 1988; Anonymous 1992; Liao 1994; Cao et al. 1995).

Taxon	Latitude (°N)	Longitude (°E)	Altitude (m)		Forest
			E. of 107 °E	W. of 107 °E	
Fagus chienii Cheng	33	104		1300	mixed forest
F. engleriana Seem.	27.5–34.3	102.2–119.4	1000–2000	1200–2500	mixed forest or rare pure stands
F. hayatae Palib. ex Hayata	24.7	121.4	1300–1500		associated with *Trochodendron, Illicium, Mahonia, Adinanthera* and *Daphniphyllum* etc.
F. hayatae var. *zhejiangensis* Liu et Wu	28.2	120.8	850		broadleaved forest
F. longipetiolata Seem.	22.3–32.7	101.2–121.5	300–1500	800–2500	mixed evergreen and deciduous broadleaved forest
F. lucida Rehd. et Wils.	24.3–32.0	103.2–120.8	800–2000	1800–2200	pure stands or mixed with other moutainous deciduous broadleaved trees
F. pashanica Yang	30.3	119.4	900–1000		mixed forest
	32.7–33.5	105–107		1200–1900	mixed needle/deciduous broadleaved forest; rare pure stands.

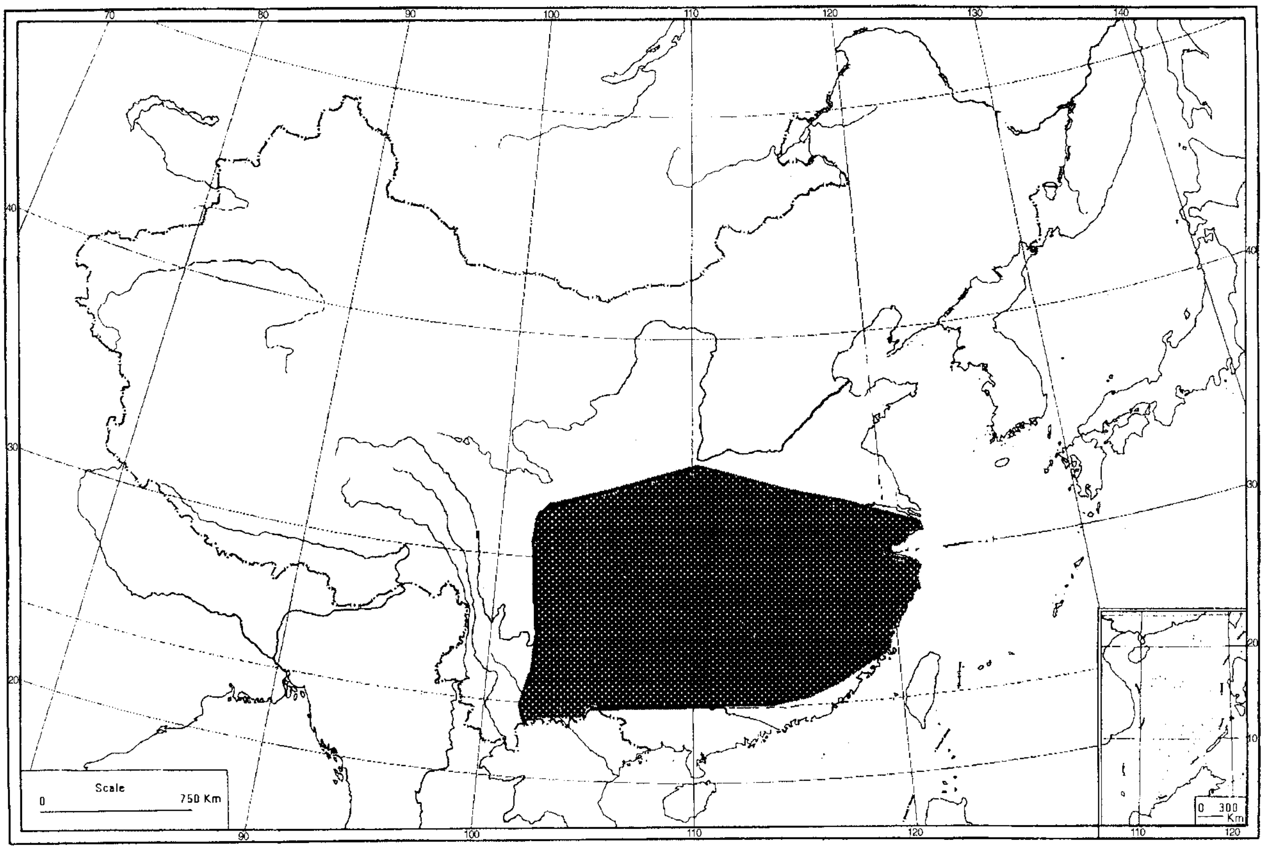

Fig. 1. Distribution of living *Fagus* in China (after Tsien et al. 1975; Chang & Huang 1988; Hong & An 1993; Cao et al. 1995; Peters 1997)

The principal factor controlling the distribution of Chinese beeches is the precipitation during the growing season, while the temperature condition is another important factor (Hong & An 1990). It is therefore reasonably explained that Chinese beeches are limited by a moisture deficit in the north, and by high temperatures plus relatively low moisture levels in the south (Cao et al. 1995). Of course, soil conditions can also be important (Zhou & Li 1994).

Table 2
Ecological comparison of *Fagus* species in China, Japan, Europe and North America (after Cao et al. 1995).

Taxon	Mean annual temperature (°C)	Precipitation (mm)
Fagus chienii Cheng	12.0–13.0	980–1150
F. engleriana Seem.	4.8–13.9	740–2400
F. hayatae Palib. ex Hayata	12.0–17.0	2800–3500
F. hayatae var *zhejiangensis* Liu et Wu	12.5–16.5	2800–3500
F. longipetiolata Seem.	6.0–16.7	850–2770
F. lucida Rehd. et Wils.	7.4–14.2	1200–2700
F. pashanica Yang	6.6–9.6	1300–1550
F. crenata Blume	3.0–13.0	1200–3400
F. sylvatica Linn.	2.0–14.0	500–2000
F. grandifolia Ehrh.	3.0–21.0	760–2100

3. Forest types: Beech species are mainly canopy elements in the subtropical montane region of China. Although these forests share some genera with other beech forests in the North Hemisphere, they are not homogeneous in species composition because of different floral development and climatic change in the geological past (Zhou & Li 1994; Peters 1997; for full list of species composition, refers to Peters 1997).

Based on the composition of tree species cooccurring with beeches in the canopy, Peters (1997) recognized three major beech forest groups worldwide in which can be further subdivided into about fourteen beech forest types. The three groups are characterised as follows:

I. beech species appearing with evergreen coniferous species – which can be found in North America, Turkey, Europe and Japan;
II. beech species co-occurring with deciduous broadleaved species – which can be seen in North America, Europe, Japan and China;
III. beech species living with evergreen broadleaved trees – which can be seen in U.S.A., Mexico, Japan and China.

There are two types of beech forests in China (Zhou & Li 1994; Peters 1997). In southern China (about 25–30 °N), beech species like *Fagus lucida* or *F. longipetiolata* occur with evergreen and deciduous trees. Evergreen genera are like *Manglietia* and *Michelia* (Magnoliaceae), *Illicium* (Illiciaceae), many genera of the Lauraceae and the Theaceae, *Castanopsis, Cyclobalanopsis,* and *Lithocarpus* (Fagaceae), *Symplocos* (Symplocaceae), *Elaeocarpus* (Elaeocarpaceae), *Idesia* (Flacourtiaceae), *Clethra* (Clethraceae), *Nyssa* (Nyssaceae), *Mallotus* (Euphorbiaceae), *Daphniphyllum* (Daphniphyllaceae), *Rhus* (Anacardiaceae), while deciduous genera include *Cercidiphyllum* (Cercidiphyllaceae), *Liquidambar* (Hamamelidaceae), *Betula* (Betulaceae), *Rhododendron* (Ericaceae), *Prunus, Photinia,* and *Eriobotrya* (Rosaceae), and *Acer* (Aceraceae). On the other hand, in the regions of 28–32 °N of central-southern China, beech forests are dominated by *Fagus lucida* (south), *F. hayatae* (north), *F. engleriana* and some other deciduous genera such as the conifers *Pinus* and *Abies, Carpinus* and *Betula* (Betulaceae), *Quercus* and *Castanea* (Fagaceae), *Tilia* (Tiliaceae), *Prunus, Sorbus,* and *Photinia* (Rosaceae), *Cornus* (Cornaceae), *Hovenia* (Rhamnaceae), *Aesculus* (Hippocastanaceae), *Acer* (Aceraceae), *Juglans* and *Platycarya* (Juglandaceae). Evergreen genera such as *Magnolia* (Magnoliaceae), *Cyclobalanopsis* (Fagaceae), *Nyssa* (Nyssaceae) also occur although they are only a few (Tsien et al. 1975; Zhou & Li 1994; Peters 1997).

It is evident that numerous genera which are comparatively commonly encountered in the Tertiary floras of China seem not to be present in modern Chinese beech forests (see Liu et al. 1996). According to Peters (1997), these genera include *Picea* and *Tsuga* (Pinaceae), *Taxus* (Taxaceae), *Ostrya* (Betulaceae), *Morus* (Moraceae), *Amelanchier* (Rosaceae), *Cercis* and *Gymnocladus* (Leguminosae), *Phellodendron* (Rutaceae), *Carya* (Juglandaceae) and *Aralia* (Araliaceae), and several genera of the Ulmaceae, e.g., *Ulmus, Celtis* and *Zelkova*.

In summary, there are mainly two basic types of beech forests in the subtropic montane region of south China. They occupy the region ranging from south of 32 °N to north of 20 °N and at altitudes from 700 to 2500 m. One type of the beech forest is characterized by the co-occurrence with dominant deciduous trees although some evergreen broadleaved species are also present, whereas the another is the main type of Chinese beech forests in which more evergreen trees present with beeches. Chinese beeches are quite susceptible to both humidity, temperature and soil conditions.

Fossil beech forests in China

Fossil records of *Fagus*, especially the pollen grains are quite common throughout China from the Late Cretaceous onwards (Tables 3 and 4). However, it is necessary to mention that the microfossils of *Fagus* in China never dominated in any pre-Quaternary assemblage although they might reach their acme in the Miocene or maybe late in the Pliocene (Pliocene fossil beeches are rarely recovered in China). This is also partly supported by a handful of macrofossils assignable to this genus from China. Hence, the lower abundance of *Fagus* in Chinese pollen diagrams may not be biased by sampling. Several explanations can be given. First, it could be that the Chinese *Fagus* had only been in a subordinate position in the ancient forests and never formed pure stands like today because of failure in competition with other trees (see Cao et al. 1995). Evergreen and/or deciduous trees were probably well-developed throughout the Tertiary in China as in many areas where fossil *Fagus* were found. Consequently, the beech fossil pollen constitute only a relatively low percentage in an assemblage. Secondly, the ancient *Fagus* in China would be prosperous, but restricted to a fairly high montane region which limits the possibility to be fossilized. In addition, this supposal could not explain why a lot of fossil beeches are frequently recovered in the adjacent areas like Japan (see Tanai 1974). Thirdly, in several cases beech fossils have not been recognized as such and were misidentified. As far as the pollen morphology of beeches is concerned, it is generally clear enough to enable a correct identification when dealing with fossil pollen, although modern palynologists sometimes do not agree on some morphological characters of *Fagus*, e.g. the colpus morphology (see Praglowski 1982; Wang & Chang 1991). Furthermore, beech leaf fossils are sometimes easily wrongly identified (Tanai 1974; Liu et al. 1996). According to the data available, we tend to support the first hypothesis.

1. Fagus in the Cretaceous: There are two published Late Cretaceous records of *Fagus* pollen grains of northeast (Anonymous 1976; Yu et al. 1983) and southeast China (Song et al. 1986), respectively (Fig. 2). In both cases *Fagus* occurs in an extremely low percentage (Table 3). The

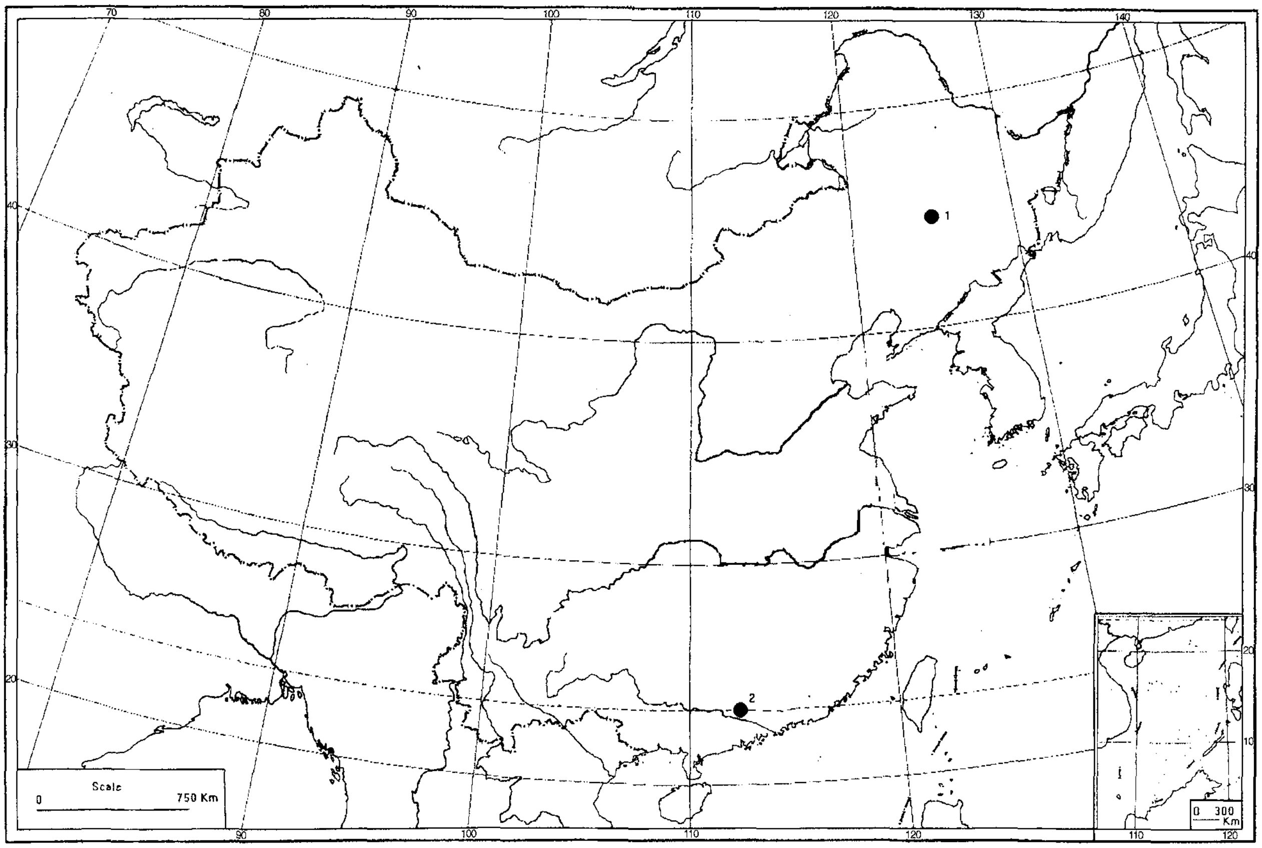

Fig. 2. Occurrences of *Fagus* in the Cretaceous (the Arabic numerals correspond to the number of localities in Table 3)

identification of these fossil pollen grains might however be questionable as Song et al. (1986) stated that the fossil species (named as *Faguspollenites tenuis* Song, Li et Zhong, 1986) from southeast China shows only a morphological resemblance with *Faguspollenites* and its relationship with *Fagus* is still unclear. As the two samples are not available for us, we can not discuss them further. Nevertheless, it may be possible that the ancestors of *Fagus* appeared in the Late Cretaceous because in the Palaeocene *Fagus* was already widely distributed (Fig. 3).

2. Fagus in the Palaeogene: The distribution of *Fagus* in the Palaeogene was the widest through the whole geological history of beeches in China (Figs 2–5) in spite of the normally fairly low abundances. Most of the fossils are pollen (Table 3), whereas only a few are leaves (Table 4).

There are no megafossils of *Fagus* found in the Palaeocene, but the pollen grains of the genus seem to occur throughout the country except for southwest China (Fig. 3), however in fairly low percentages. The highest percentage recorded (5%) is from the southern part of the country – Sanshui Basin of Guangdong Province (Song et al. 1986). The Palaeocene beeches seem to live in two completely different climates (Guo 1985, 1990). One is a moist and warm temperate climate in the northeast (Liu 1983), while the other is a torrid and arid climate in the central and south (Li 1980; Wang & Zhao 1980; Song et al. 1981, 1985, 1986; Zhao 1982; Wang et al. 1987; Wang 1990). Neither of the climates appear not to fit in with the ecological requirements of modern beeches. Floristically, associated taxa in the fossil floras are quite different with those in the living beech forests. For example, one palynoflora from Jiayin County, northeast China has the following dominant members: Betulaceae, Ulmaceae, Juglandaceae and Myricaeae (Liu 1983). However, Ulmaceae and Myricaeae no longer occur in the Chinese living beech forests (Peters 1997).

In the Eocene, fossil leaves of *Fagus* are found in southwest China (Table 4, Fig. 4; Zhang 1983; Liu et al. 1996). However, because of their poor preservation, these fossils can not be definitely assigned to *Fagus*. On the other hand, the pollen records reveal more complete distribution patterns than the leaves. And again, the occurrences of the Eocene beech pollen are still low. Additionally, it is strange that beeches seem to

Table 3
Occurrences of fossil *Fagus* pollen in the pre-Quaternary of China (mostly based on Wang Wei-Ming unpublished data).

Locality	Stratum	Age	Content (%)	Reference
1. Songliao Basin, N.E. China	Mingshui Form.	Maastrichtian	0–1.2	Anonymous 1976; Yu et al. 1983
2. Sanshui Basin, S.E. China	Dalangshan Form.	Late Cenomanian-Maastrichtian	sparse	Song et al. 1986
3. Jiayin, N.E. China	Wuyun Form.	Late Palaeocene	sparse	Liu 1983
4. Coastal region of Bohai Sea and Bohai Sea, N.E. China	Shahejie and Dongying Form.	Late Eocene-Oligocene	0–1.2	Anonymous 1978; Guan et al. 1989; Yamanoi et al 1993
5. N. Jiangsu, E. China	Uppermost of Taizhou Form.	Danian	0–1.0	Song et al. 1981; Zhang & Qian 1992
	Funing Form.	Late Palaeocene	0–1.0	
	Dainan Form.	Early Eocene	sparse	
6. Hefei Basin, E. China	Dingyuan Form.	Palaeocene-Eocene	0–3.1	Wang et al. 1987
7. Shelf Basin of East China Sea	Lingfeng Form.	Late Palaeocene	sparse	Song et al. 1985;
	Huagang Form.	Oligocene	0–1.2	Anonymous 1989
8. Cixi, E. China	Changhe Form.	Palaeocene-Eocene	sparse	Li 1980
9. Nanling, E. China	Shuangta Group	Oligocene	sparse	Wang et al. 1987
10. Jianghan Area, C. China	Xingouju Form.	Palaeocene-Eocene	sparse	Wang & Zhao 1980;
	Qianjiang Form.	Middle-Late Oligocene	1–2.0	Li et al. 1978
11. Songci, C. China	Yangxi and Pailoukou Form.	Eocene	sparse	Lei et al. 1987
12. Sanshui Basin, S.E. China	Buxin Group	Palaeocene	0–5.0	Song et al. 1986;
	Xibu Form.	Early Eocene	sparse	Li & Qing 1994
13. Xining-Minghe Basin, N.W. China	Qijiachuan Form.	Palaeocene Early Eocene	0–1.0	Wang et al. 1990
	Honggou Form.	Eocene	0–2.0	
14. Changdu, S.W. China	Gonjo Form.	Late Eocene	sparse	Song & Li 1982
15. Kuche Basin, N.W. China	Talake Form.	Early Palaeocene	1.0–2.0	Zhao et al. 1982
	Xiaokuzibai Form.	Early Eocene	2.0	
	Suweiyi Form.	Middle-Late Eocene to Early Oligocene	1.0	
16. Tarim Basin,	Wulageng Form.	Middle Eocene	sparse	Wang et al. 1990
17. Coastal region of Bohai Sea and Bohai Sea, N.E. China	Guantao Form.	early Middle Miocene	0–6.7	Anonymous 1978;
	Minghuazhen Form.	Miocene-Pliocene	0–7.6	Guan et al. 1989; Yamanoi et al 1993
18. Shanwang Basin, E. China	Shanwang Form.	early Middle Miocene	2.8–8.1	Liu 1986; Liu & Leopold 1992
19. N. Jiangsu, E. China	Lower Yancheng Group	early Middle Miocene	0–1.0	SONG et al. 1981
20. Tianchang, E. China	Strata unnamed	Early Miocene	1.3–3.0	Zheng & Zhang 1986
21. Fuyang Area, E. China	Strata unnamed	Miocene	0.8–1.2	Wang et al. 1987
22. Shelf Basin of East China Sea	Hailonging and Yuquan Form.	Miocene	sparse	Song et al. 1985; Anonymous 1989
	Santan Form.	Pliocene	0–1.8	
23. E. Zhejiang, E. China	Strata unnamed	Miocene	0–1.6	Wang et al. 1985; Zheng 1982
24. Yalong, S.W. China	Strata unnamed	late Early Miocene-early Middle Miocene	0.9–1.0	Wang 1989
25. Zhaotong, S.W. China	Strata unnamed	Early Pliocene	0–3.2	Song 1988

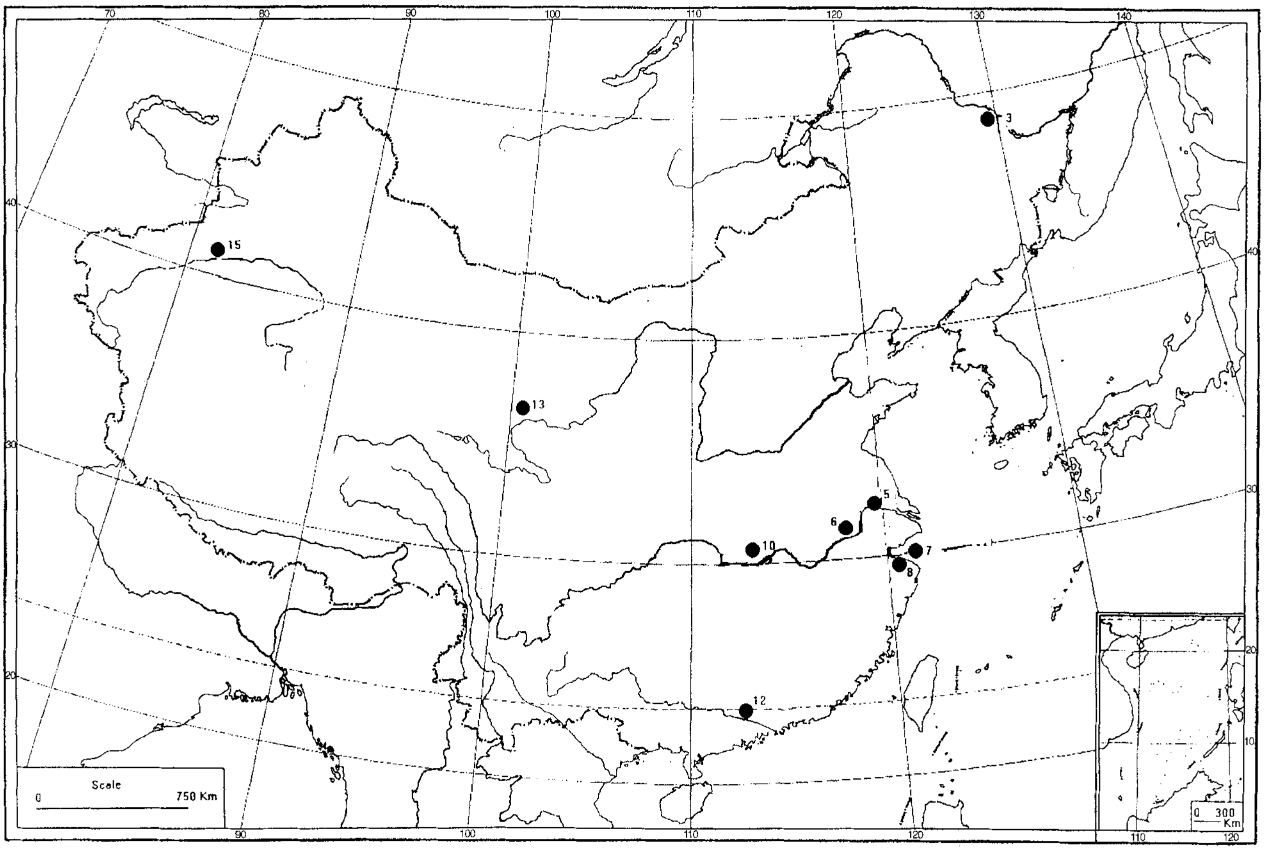

Fig. 3. Occurrences of *Fagus* in the Palaeocene (the Arabic numerals correspond to the number of localities in Table 3)

retreat from northeast China, where climate was still humid and warm then (northern subtropical or warm temperate conditions) (Guo 1985, 1990). The difference in distribution of *Fagus* with that in the Palaeocene is that beeches seem to invade further south to the southwest (Song & Li 1982; Zhang 1983) and west to the northwest (Wang et al. 1990). All the Eocene beeches occupy the areas with an arid and subtropical climate (Guo 1985, 1990; Li & Zheng 1995). It is not easy to understand why *Fagus* as a typical hygrophilous genus could survive there because

Table 4
Summary of megafossil species of *Fagus* in China (mostly based on Liu et al. 1996; Leng 1997).

Locality	Taxon	Age	Occurrence	Reference
26. Panxian, S.W. China	*Fagus* sp. 1	Late Eocene to Early Oligocene	2 fragments	Zhang 1983
27. Yanji, N.E. China	*F. galbanifolia*	Late Oligocene	8 leaves	Guo 1992
	F. sp. 2	Late Oligocene	3 leaves	Guo 1992
28. Weichang, N.E. China	*F. engleriana*	Miocene	several leaves	Depape 1932
29. Dunha, N.E. China	*F. stuxbergi*	Middle Miocene	13 leaves	Li & Yang 1984
30. Huanan, N.E. China	*F. altaensis*	Middle-Late Miocene	19 leaves	Leng 1997
	F. antipofii	Middle-Late Miocene	16 leaves	Leng 1997
	F. florinii	Middle-Late Miocene	1 fragment	Leng 1997
	F. silesiaca	Middle-Late Miocene	3 fragments	Leng 1997
	F. sp.	Middle-Late Miocene	1 fragment	Leng 1997
31. Nanfeng, S.E. China	*F. praelucida*	Pliocene	1 leaf	Li & Guo 1982
32. Panxian, S.W. China	*F.* sp. 3	Early Pleistocene	some cupules	Zhang 1978

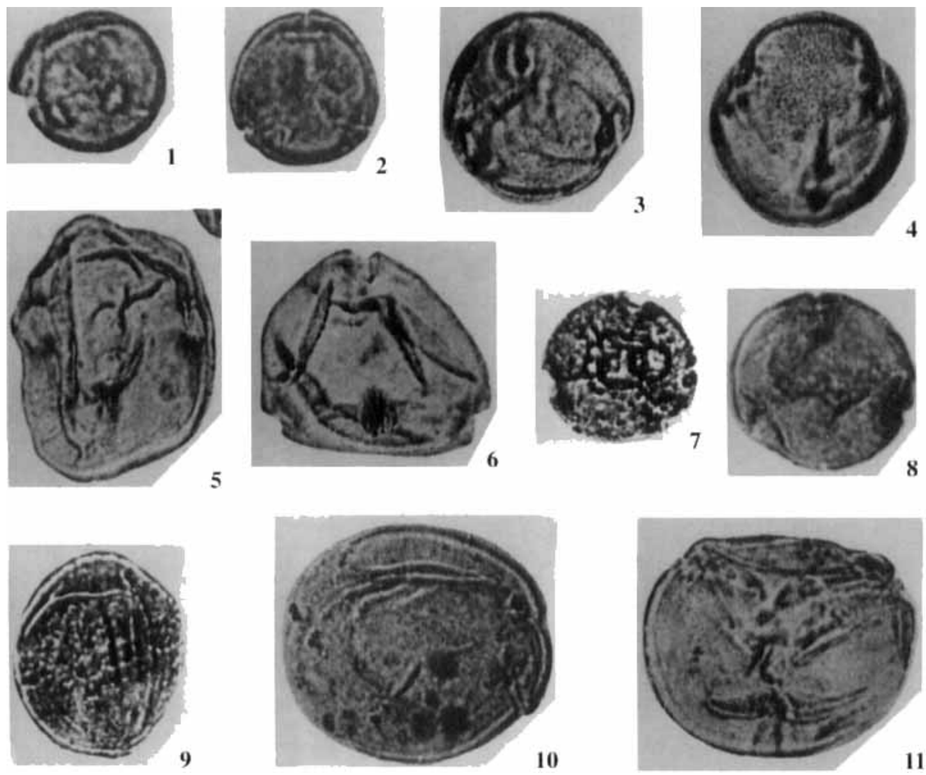

Plate. **1, 2**. *Faguspollenites parvifossilis* (Traverse) Yu, Gao et Mao – North of Jiangsu Province, southeast China; Palaeocene, Taizhou Formation. **3, 4**. *Faguspollenites mediocris* Zheng – Bohai Sea; Miocene, Guantao Formation. **5, 6**. *Faguspollenites changheensis* Li – Cixi County, northeastern Zhejiang Province, southeast China; Palaeocene-Eocene, Changhe Formation. **7, 8**. *Faguspollenites verus* Raatz. **7**. Coastal region of Bohai Sea; Late Eocene, Shahejie Formation; **8**. Songci County, Hubei Province, central China; Eocene, Pailoukou Formation. **9**. *Faguspollenites pseudocruciatus* Potonie – Jianghan Plain, Hubei Province, central China; Oligocene, Qianjiang Formation. **10, 11**. *Faguspollenites koraiensis* Takahashi – Shelf basin of East China Sea. **10**. Pliocene, Santan Formation; **11**. Miocene, Yuquan Formation

humidity must have been fairly low and temperature quite high for *Fagus* (Guo 1985, 1990; Zhang 1990; Li & Zheng 1995). Moreover, the big and oily seeds of *Fagus* do not likely germinate if they are exposed to dry conditions for a longer period of time (Hong & An 1993). The only explanation is that the ecological requirements of the ancient *Fagus* may have changed. If that is the case, *Fagus* in the past could have been adapted to wider water and heat requirements than the extant beeches, and of course this must be a good example that palaeoclimatic reconstruction by means of comparison with living equivalents should be considered with caution. Another possibility is that the dry and warmer climates are not as severe as has been assumed and they are probably not beyond the ecological tolerance of *Fagus*. Unlike fossil leaves, palynological data are somewhat limited to allow palaeoclimatic reconstruction quantitatively. Therefore, more macrofossil materials especially leaves are required to evaluate further the palaeoecological parameters of *Fagus* (see Wolfe 1993).

Oligocene floras are relatively rare in China. However, both the beech leaves and the pollen from the Oligocene show significant distribution patterns (Fig. 5). It is very obvious that beeches seemed to return to northeast China in the Late Oligocene. In northeast China, only megafossils of *Fagus* are reported from a single flora (Guo 1992). The leaves are the earliest undoubted macrofossil records of *Fagus* from China. These fossils include at least two leaf types in which one type is near to *Fagus lucida* Rehder et Wilson and the other to *F. engleriana* Seemen and *F. multinervis* Nakai (Liu et al. 1996). *Fagus multinervis* Nakai is now endemic to Ulleung-do Island of South Korea. The Oligocene beech leaves from northeast China appear to be similar to the East Asian species only. In addition, the Oligocene flora shares numerous genera (e.g. *Pinus, Castanea, Quercus, Acer*, some members of Rosaceae and Leguminosae) with the living beech forests (see Guo 1992). As far as pollen records of *Fagus* from other parts of China are concerned, their occurrences are again very low in every assemblage (Li et al. 1978; Zhao et al. 1982; Wang et al. 1987; Anonymous 1989).

The climatic cooling in the Oligocene probably explains why beeches reappeared in northeast China. This is simply because beeches request moderate temperature and much humidity. In northeast China, the climate in the Eocene was warmer and somewhat drier than that in the Palaeocene (Guo 1985). Therefore, the beeches might temporarily disappear there in the Eocene.

From a floristical point of view, the Early Tertiary fossil floras containing beeches from south-central China appear to share numerous genera with the living beech forests (e.g. *Quer-*

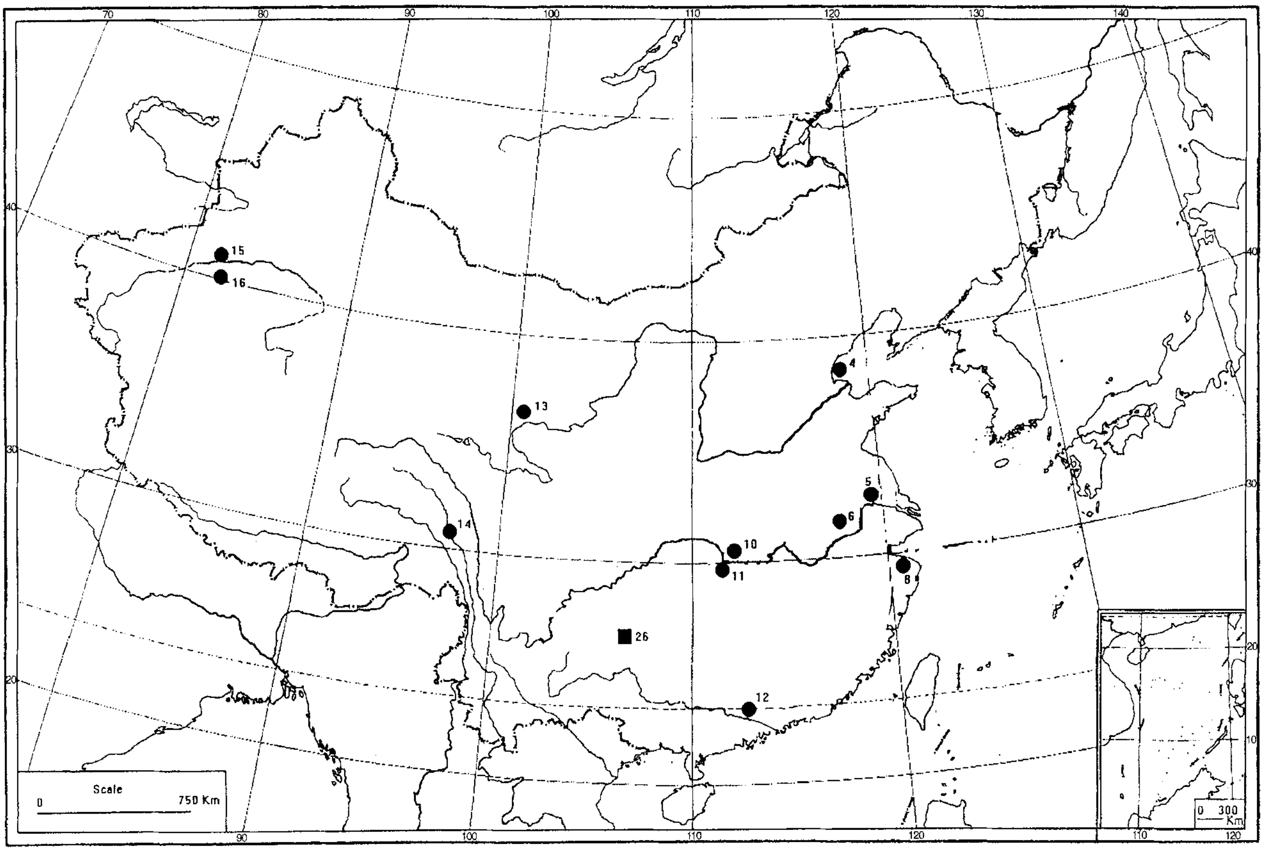

Fig. 4. Occurrences of *Fagus* in the Eocene (the Arabic numerals correspond to the number of localities in Tables 3, 4). Round dot = fossil pollen, and square = megafossil

cus, Nyssa, Symplocos, Rhus, Betula, Carpinus, and *Fraxinus*). But the difference is still very big. A number of genera which are now not found in the living beech forests any more are often dominant in those fossil floras. These genera include, e.g. *Ulmipollenites* (Ulmaceae) (Anonymous 1978; Wang & Zhao 1980; Song et al. 1981, 1986), *Lonicerapollenites* (Caprifoliaceae) (Song et al. 1986), *Engelhardtioidites, Caryapollenites* (Juglandaceae) (Anonymous 1978; Song et al. 1981; Song & Li 1982), *Alnipollenites* and *Ostryoipollenites* (Betulaceae) (Song et al. 1981), *Myricipites* (Myricaceae) (Wang & Zhao 1980), *Myrtacidites* (Myrtaceae) (Song et al. 1986), *Araliaceoipollenites* (Araliaceae) (Wang & Zhao 1980), and *Liquidambarpollenites* (Hamamelidaceae) (Anonymous 1978).

In addition, the fossil forests containing *Fagus* seem to have been much more diverse than the living ones. As stated above, the living beech forests in China are generally attributed to mixed evergreen and deciduous broadleaved forests. Conifers and xerophytes do not occur in the living forests. However, coniferous or/and xerophilous species such as *Cedripites, Podocarpidites, Pinuspollenites, Pterisisporites,* and *Ephedripites* appear to be quite common in the beech-containing fossil assemblages, particularly in the northwestern part of China (see Zhao et al. 1982; Wang et al. 1990). Therefore, the fossil evidence from the Palaeogene of China shows a great difference existing between the fossil beech forests and the living ones.

In conclusion, Palaeogene *Fagus* always appears in a low percentage in every flora. That may suggest that *Fagus* in China had never taken a key place in ancient floras during the Early Tertiary. *Fagus* might first appear in China in the Late Cretaceous. In the Palaeocene, *Fagus* was widely distributed in different climates. But it further expanded its distribution southward in the Eocene while it retreated from the northeast. They seemed to survive in a dry and warm climate during that period. Beeches could be back to northeast China during the Oligocene worldwide climate cooling. Therefore, Palaeogene beeches lived in different habitats and associated with dissimilar plants as compared with the living beeches.

3. Fagus in the Neogene: In the Late Tertiary, the distribution of *Fagus* was strongly re-

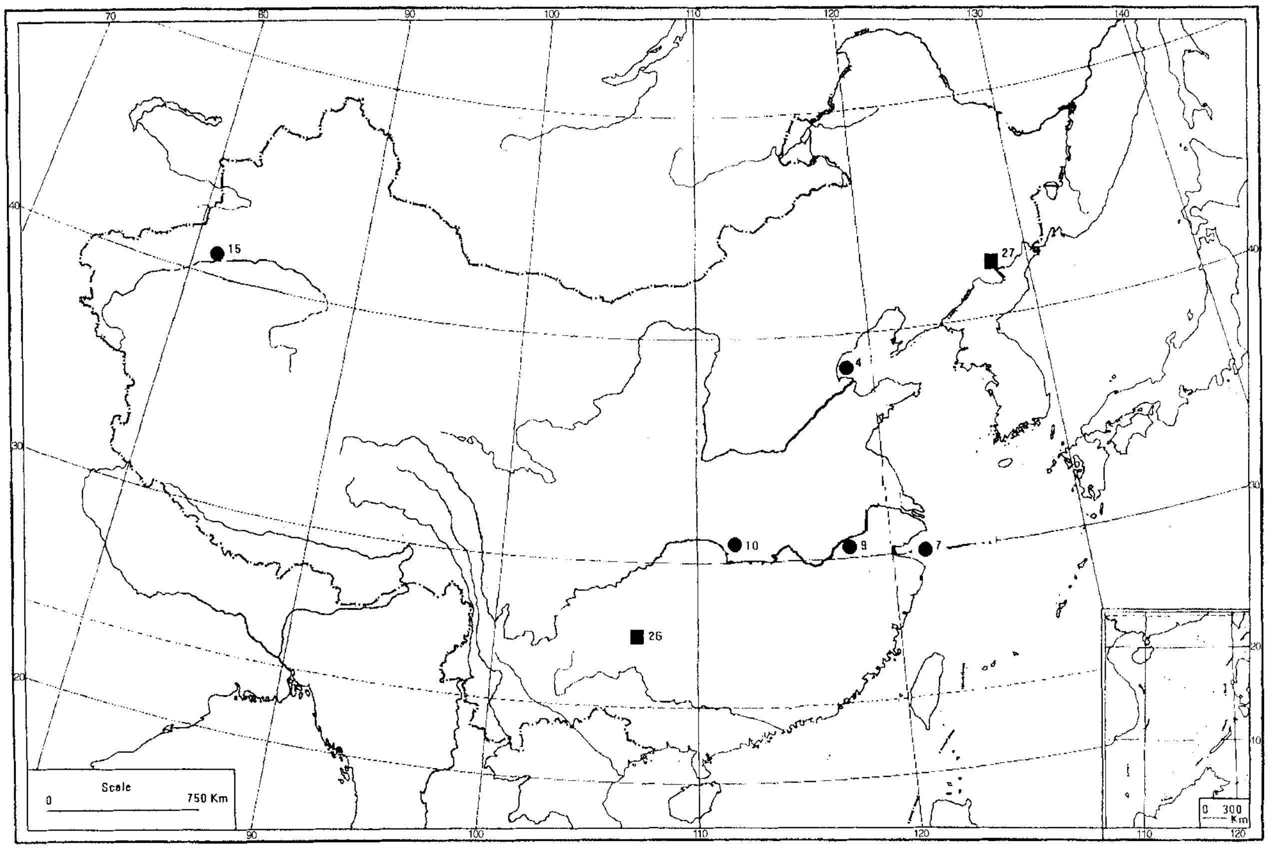

Fig. 5. Occurrences of *Fagus* in the Oligocene (the Arabic numerals correspond to the number of localities in Tables 3, 4). Round dot = fossil pollen, and square = megafossil

duced and confined to the eastern part of China (Figs 6, 7). The retreat of *Fagus* seems to be in accordance with the climatic changes in East Asia due to the Himalayan movements since the Oligocene (see Yin et al. 1988). The atmospheric currents changed completely by the uplift of the Himalayan Mountains. That enhanced the monsoon climate in east China and the continental climate in northwest and northern China (Hong & An 1993). That might explain the absence of *Fagus* fossils in northwest China (see Wang 1994).

There are rare pollen records of *Fagus* from the northern part of east China, where all the Chinese Miocene *Fagus* leaves are found (see Depape 1932; Li & Yang 1984; Liu et al. 1995). In that area, there seem to have been no more subtropical floras after the Oligocene (Guo 1985, 1990; Zhang 1995). The fossil leaves show the highest diversity morphotypic and specific in the Chinese Tertiary (Table 4; Liu et al. 1996; Leng 1997). A good example is the study of five leaf species from Huanan County, northeast China (Leng 1997). The five species are *Fagus antipofii* Heer, *F. altaensis* Kornilova et Rajushk., *F. florinii* Huzioka et Takahashi, *F. silesiaca* Walther et Zaskawniak and *Fagus* sp. The former three species are common elements in the East Asian Tertiary floras. The occurrence of *Fagus silesiaca* in China is very interesting as the species is common in the European Mio-Pliocene (Walther & Zaskawniak 1991). This indicates that during the Miocene floristic exchanges between China and other parts of Eurasia occurred. However, the species composition of these Chinese Miocene floras is still very different from that of modern beech forests, e.g. the flora from Dunhua County, northeast China (Li & Yang 1984). The Miocene flora is considered as a mixed northern hardwood and flourishing in a warm temperate climate (Liu & Zheng 1995), which is completely different from the modern Chinese beech forests. Except for a single conifer genus (*Pinus*), all the other seven out of fourteen genera (*Pseudolarix, Cunninghamia, Glyptostrobus, Sequoia, Taxodium, Metasequoia* and *Cupressus*) can not be found any more in the living beech forests in China. A recently found flora from Huanan County (Liu et al. 1995) also shows similar difference.

Palynological records reveal similar trends of beech forest development. The percentage of

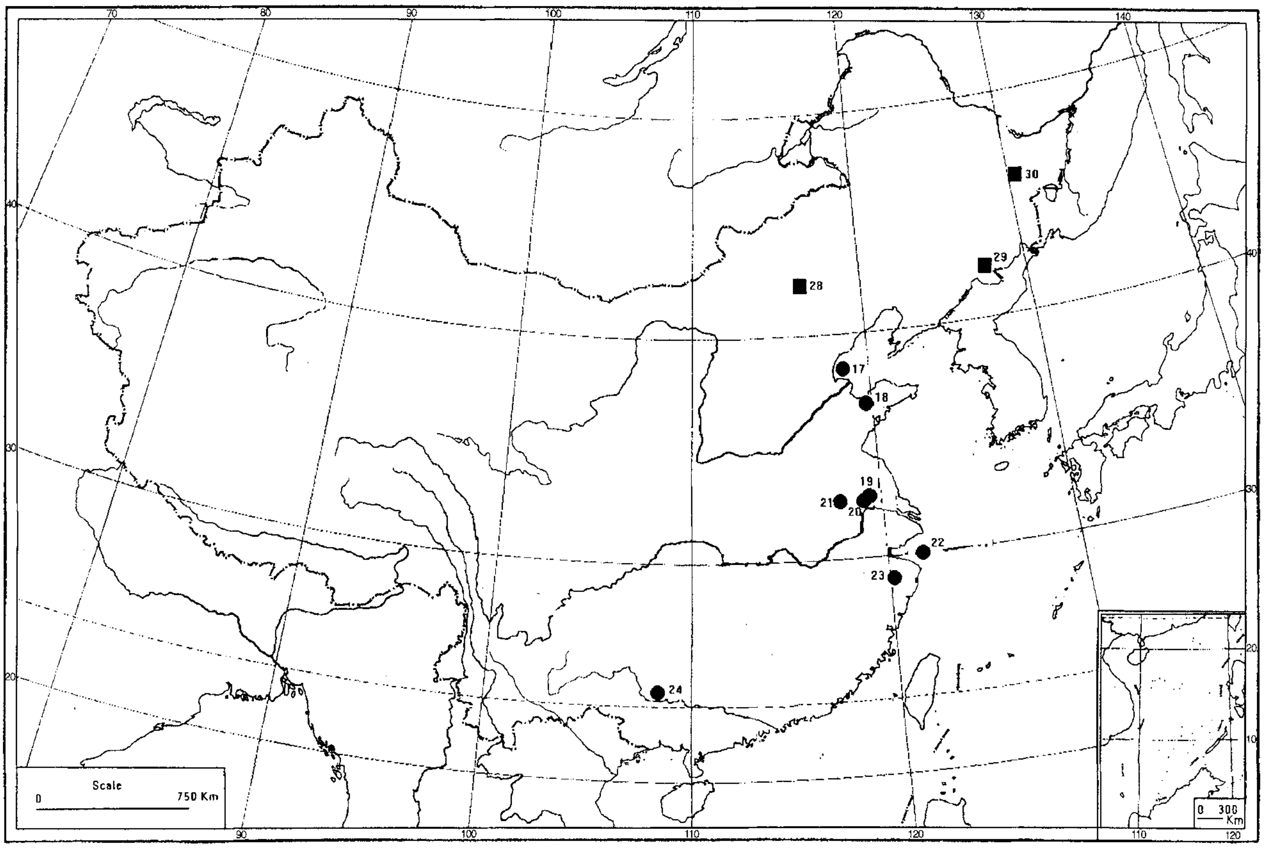

Fig. 6. Occurrences of *Fagus* in the Miocene (the Arabic numerals correspond to the number of localities in Tables 3, 4). Round dot = pollen record, and square = megafossil. Fossil pollen grains of *Fagus* have also been discovered in Huanan County (round dot = No. 30), but they have not been reported in detail yet (see Liu et al. 1995)

Fagus pollen in most of assemblages has fairly increased during the Late Tertiary (Table 3). The Shanwang flora has the highest percentage of *Fagus* varying between 2.8 to 8.1% (Liu & Leopold 1992). These latter authors pointed out that the flora should favor the flourish of *Fagus* as both the temperature (mean annual temperature = 13.5–16.6 °C) and water (annual precipitation = ca. 1,000 mm) conditions could be optimum for *Fagus* (cf. Cao et al. 1995). However, the dominant elements in that flora are *Pinus* (7.2–11.7%), *Quercus* (10–19%), *Ulmus* (7.6–16.0%), *Juglans/Pterocarya* (5.4–11.6%) and *Carya* (5.6–8.4%). Furthermore, no fossil leaves of *Fagus* have been found in the same strata for at least half a century (Liu et al. 1996).

Unlike in the Palaeogene, there were fewer types of forests containing beeches in the Miocene although more diverse forests had got to be developed as the then climatic differentiation resulted in a large vegetational differentiation in China during the Late Tertiary (see Wang 1994). During the Miocene, for instance, a subtropical climate controlled most of east China, where vegetations consisted of mixed coniferous and deciduous broadleaved forests in the north (Anonymous 1978a; Guan et al. 1989; Yamonoi et al. 1993), mixed evergreen and deciduous broadleaved forests in the central area (Song et al. 1981, 1985; Zheng & Zhang 1986; Liu & Leopold 1992) and evergreen broadleaved forests in the south (Wang 1989). These forests began to resemble the modern beech forests though the species composition is still different (see Song et al. 1981; Wang et al. 1985; Zheng & Zhang 1986; Wang 1989; Liu & Leopold 1992).

Pliocene floras containing *Fagus* are rare (Fig. 7). *Fagus* is again absent in northeast and even in north China because of severe cooling and a dry climate (Liu 1988), but it occurs along the east coast, in the southeast and in montane regions of southwest China (Anonymous 1978, 1989; Li & Guo 1982; Song 1988). Moreover, their percentage in fossil assemblages decreases again. The scarce information on Pliocene floras in China may be due to the fact that only few floras have been studied (Liu 1988). Therefore, it is possible that Pliocene *Fagus* was more widely distributed in southern China than is revealed by the data presently available.

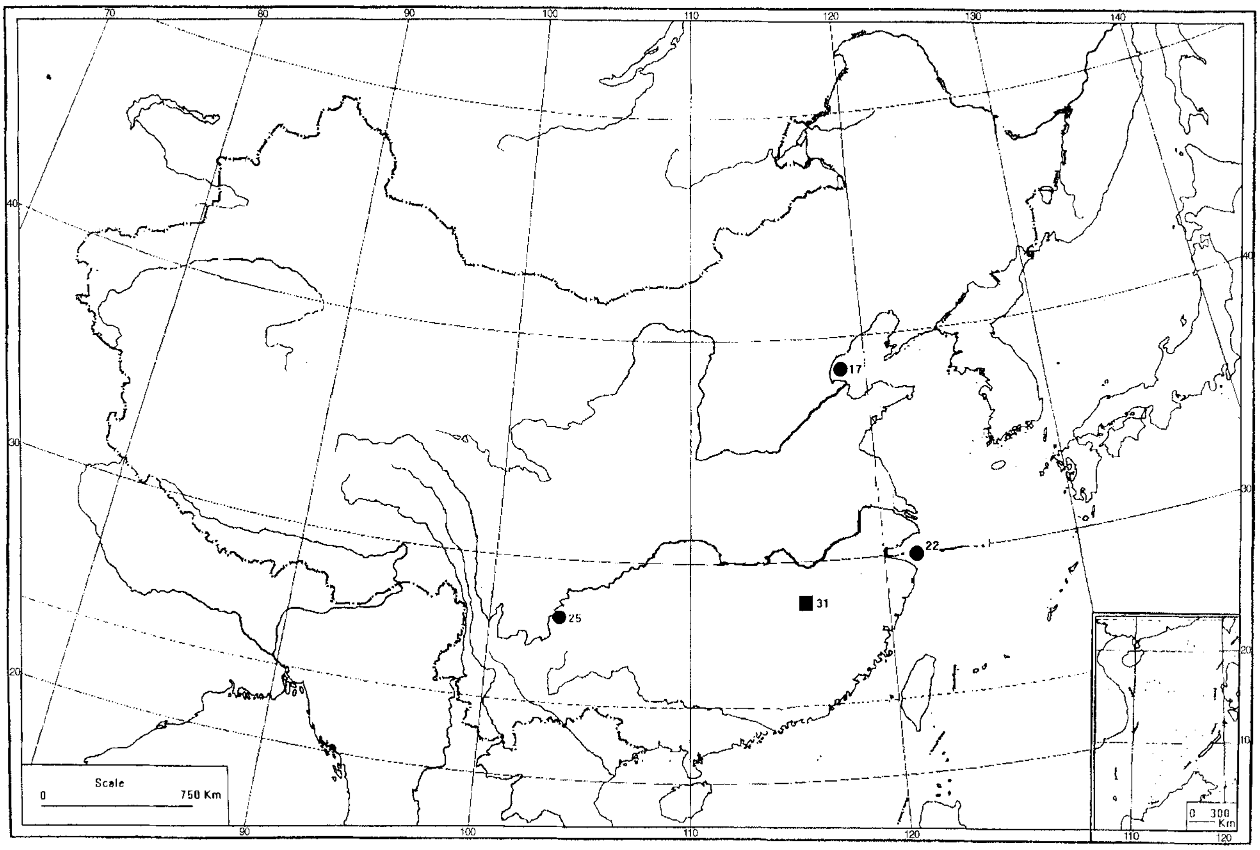

Fig. 7. Occurrences of *Fagus* in the Pliocene (the Arabic numerals correspond to the number of localities in Tables 3, 4). Round dot = pollen record, and square = megafossil.

In summary, the distribution of beeches in China was more restricted in the Neogene than during the Palaeogene. In the Miocene *Fagus* is most abundant in pollen assemblages and the diversity of leaf types. In comparison to the European Neogene, the proportion of beeches is still very low in China. Srodon (1985) reported that the maximum values of beech pollen in the Polish Neogene can exceed 20% and even 40%. The abundance and diversity of the Chinese beeches obviously declined in the Pliocene. However, more information is still required. In the Neogene, especially in the Miocene, beeches still lived in different forest types from the modern Chinese beech forests. However, the differences might be smaller than in the Palaeogene. Therefore, the development of a modern distribution pattern and final fixing of their ecological requirements for modern *Fagus* should have happended even after the end of the Tertiary.

Conclusions

In pre-Quaternary deposits of China, pollen grains of *Fagus* often occur in rather low percentages. They might originate in the Cretaceous when sparse records exist. The Palaeogene fossils of the genus, however, scattered throughout China. Some survived in a humid and warm habitat in the northeast, while the remainder lived under dry and torrid conditions. The ancient forests containing *Fagus* probably share minor resemblance with the modern beech forests. In the Neogene, however, the distribution of *Fagus* was largely reduced. Particularly, beeches retreated from the northern and northwestern regions of China. This is probably because those areas had become too cold and arid for beeches to exist after the Oligocene. But *Fagus* started to differentiate in east China and finally reached its peak of diversity. Exchange of *Fagus* species was then possible among China, Europe, Far East and Japan. It must be stated that it is not possible at the moment to compare the Chinese fossil beeches with those in other parts of the world due to poor preservation of the Chinese species. Based on scrappy records of beech leaf fossils from China, the Chinese beeches apparently developed more or less independently during the Tertiary. More materials however are required. In addition, the Neogene forests with *Fagus* have

Table 5
Comparison between fossil and modern beech forests in China.

Item	Palaeogene beeches	Neogene beeches	Modern beeches
1. Distribution			
(1) region	most widely	east & southwest China	south China
(2) altitude	lowland	relatively high	montane
2. Occurrence	sparse	slightly increased	dominate element/pure stands
3. Ecology			
(1) temperature	highest	higher	moderate
(2) humidity	lowest	moderate	high
4. Forest			
(1) type	most diverse	numerous	a few
(2) associate species	*Pinus, Ephedra Podocarpus,* Taxodiaceae; *Ulmus, Ostrya, Quercus, Rhus*	*Pinus, Tsuga Picea, Keteleeria; Ulmus, Carya, Juglans Alnus, Betula, Quercus* ...	*Pinus, Abies, Cathaya; Juglans,* Fagaceae, Lauraceae, Theaceae, Rosaceae ...

more genera common as compared with the modern beech forests of China. One of the most evident floristic changes is the decline of *Ulmipollenites* from a higher percentage (>15%) in the Palaeogene to a relatively low content (5–10%) in the Miocene. As we have mentioned above, taxa of the Ulmaceae are no longer found in the modern beech forests. Pliocene cooling climate might again reduce the distribution areas of *Fagus*. In a word, as its often low contents in occurrence, *Fagus* had never been an important element in the Chinese Tertiary vegetation. It is believed that the final development of the Chinese modern beech forests might be possible after the Tertiary.

The differences in distribution, floristic composition, and ecological characters between the pre-Quaternary *Fagus* and the modern ones in China are summarized in Table 5.

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