EXOCHORDA: FIVE SPECIES OR ONE?

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Cover: author. *Exochorda racemosa* (Lindl.) Rehder subsp. *racemosa*, population 01
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Gao Fangyou

Exochorda: five species or one?

A biosystematic study of the Rosaceous genus *Exochorda*

Proefschrift
ter verkrijging van de graad van doctor
op gezag van de rector magnificus
van de Landbouwuniversiteit Wageningen
dr. C.M. Karssen
in het openbaar te verdedigen
op 28 januari 1998
des namiddags te vier uur in de Aula

Promotor: Prof. Dr. ir. L.J.G. van der Maesen
Hoogleraar in de plantentaxonomie

Propositions

1. *Exochorda* populations are morphologically very similar, and appear to belong to the same species, although their distributions are clearly disjunct.
   ___ this thesis

2. The phenetic study does not support five distinct taxa (i.e. five species) in the *Exochorda* complex. Instead, three broadly defined subspecific taxa can be recognized. These coincide in part with the geographical distribution in the genus.
   ___ this thesis (page: 83)

3. *Exochorda* originated before the emergence of the Taklamakan Desert. It probably once occupied a large area in the northern hemisphere of Asia. The disjunct distribution pattern represents the relict of a former wide and continuous distribution pattern, the intervening areas having been depopulated.
   ___ this thesis (page: 106)

4. The genus *Exochorda* has been neglected for quite a long time especially in China. Its merits should become more and more appreciated for gardening.
   ___ author

5. China is one of the richest regions of plant diversity contributing many important crops, particularly fruit trees. Other important crops are *Brassica campestris* and related species, *Camellia sinensis, Colocasia esculenta, Corchorus sinensis, Glycine max, Panicum milaceum, Raphanus sativus, Setaria italica* etc.
   ___ A.C. Zeven & P.M. Zhukovsky. 1975. Dictionary of cultivated plants and their centres of diversity: 27.

6. Knowledge and experience do not necessarily speak the same language.
___ Taoist philosophy

7. Education is a lifelong process, a process that starts long before the formal start of school education, and one that should be an integral part of one's entire life.

8. Learning without thinking is useless; thinking without learning is perilous.
___ Confucius (551-479 B.C.)

9. Faith is the bird that feels the light when the dawn is still dark.
___ Rabindranath Tagore (1816-1941)

10. What everyone wants from life is continuous and genuine happiness. Happiness is the rational understanding of life and the world.
___ Baruch Spinoza (1631-1677)

Stellingen, horend bij het proefschrift van Gao Fangyou:
Exochorda: five species or one?
A biosystematic study of the Rosaceous genus Exochorda

Wageningen, 28 januari 1997

Nature brings me sunshine and music in my life.

——Author

To Prof. Dr. L.J.G. van der Maesen
To my parents
To my husband

Contents

Preface

The present dissertation has three objectives: first, to solve the question: how many species exist in the Rosaceous genus *Exochorda*: five or one?; to describe and analyze the kinds of adaptive radiations that could have given rise to morphological and anatomical differences to distinguish species in *Exochorda*; second: to compare *Exochorda* with other genera in Rosaceae, with respect to leaves, wood, pollen and chromosome, these data give us a record of taxonomic information; third: to explore the origin, dispersal and present geographical distribution of the genus and ecological factors that influence diversification.

Chapter 2 to 5 provide information for the taxonomy of the genus. In chapter 6, the embryology of *Exochorda* is treated. Chapter 7 discusses the pollination of the species. In chapter 8, molecular methods were used to attempt to detect differences between populations. In chapter 9, numerical taxonomy of *Exochorda* is performed. In chapter 10, the taxonomic revision is given. Chapter 11 presents the postulates of the origin, dispersal and present geographical distribution of the genus.

Gao Fangyou
Wageningen, the Netherlands
December, 1997

Summary

The Rosaceous genus *Exochorda* consisted sofar of five accepted species and is distributed in East Asia and Central Asia. Morphologically the taxa in the *Exochorda* complex have similar characters, hence the classification in the complex was questionable. A further problem is the relationship between the genus *Exochorda* and other genera in Rosaceae. In this dissertation, based on wild material of 22 populations in China, cultivated accessions in the botanical gardens of Wageningen Agricultural University, the Netherlands, and herbarium material, a biosystematic study of this genus is reported. The results are summarized as follows:

Leaf anatomy: The epidermis consists of one layer of cells and the shape of epidermis cells is irregular in outline as seen on both surface. Epidermal cell shape in surface view is quite uniform in *Exochorda.* Stomata are always confined to the lower leaf surface. An anomocytic pattern is found in all samples.

Wood anatomy: growth rings are distinct, boundaries are marked by differences in vessel diameter between earlywood and latewood, and by rows of flattened late wood fibres. The wood is ring-porous to semi-porous. Quantitative anatomical characters express continuous variation within the "species", wood of *Exochorda* shows a single wood structural type similar to that of the Prunoideae than to the Spiraeoideae.

Pollen morphology and exine structure show little variation in this genus. *Exochorda* pollen grains are isopolar, three-colporate, small or medium-sized, grain shape is spheroidal. P = 20.9-30.5 (19.6-36.9) µm, E = 22.1-30.7 (17.9-35.7) µm, A = 5.2-9.5 (3.6-15.5) µm, P/E = 0.88-1.36 (0.81-1.73). Ornamentation is striate. All the samples are closely grouped due to similarities in these characters. These "species" have to be regarded as one species. Compared with pollen morphology of other genera in Rosaceae, *Exochorda* pollen is similar to that of *Neillia, Sorbaria, Spiraea* and *Prunus.*

All the populations are diploid (2n = 16 or 2n = 18), both numbers are frequently in the same root tip preparation. The chromosomes are small, 1-2 µm; there is little difference between different pairs; the structure is basically metacentric; symmetry is high; no satellite chromosomes were observed.

The results of embryological investigation in this genus showed that the meiosis of the microspore mother cells is of the Simultaneous type. The tapetum belongs to the Glandular type. The mature embryo sac is of the Polygonum type.

Exochorda has a mixed mating system, inbreeding and outbreeding, and >7% of its progeny result from self-pollination. The most important vectors for pollination are honeybees, their relative abundance on the flowers and their intrafloral behaviour make them a major contributor to the reproductive success of *Exochorda.* Over 30% of the pistils degenerate during the flowering period, resulting in low fruit set. The fruit set varies from 11% to 70%.

From the RAPD results in some Rosaceae, it is concluded that five previous taxa (five species) of *Exochorda* are not clearly separated. Instead, all *Exochorda* samples were defined in one group and are distinct from other genera in Rosaceae. These data indicate that the interspecific relationships in *Exochorda* are not very clear. The RAPD data also disturb the common opinion regarding the traditional subfamilies in Rosaceae. At least some of the four subfamilies as separate taxonomic units in Rosaceae are quite heterogeneous.

The findings in multivariate analysis point to a continuous variation of morphological characters. This analysis supports the opinion that overall differences are small within the *Exochorda* complex. The multivariate analysis does not support five distinct taxa (species) in the *Exochorda* complex, but three loosely defined taxa can be recognized. *E. korolkowii*, *E. tianshanica* and *E. racemosa* appear conspecific. *E. korolkowii* and *E. tianshanica* are united with *E. racemosa* and treated as synonyms.

The results obtained in the earlier chapters are used in the revision to delimit taxa. It is concluded that all the taxa belong to one species. The original five different "species" are reduced to three subspecies, i.e. *E. racemosa* (Lindl.) Rehder subsp. *racemosa*, subsp. *giraldii* (Hesse) F.Y. Gao & Maesen and subsp. *serratifolia* (S. Moore) F.Y. Gao & Maesen.

This genus does not fit in any of the four classical subfamilies in Rosaceae. A tribal status as Exochordeae is more suitable.

Exochorda has a relatively narrow and disjunct distribution limited to East Asia and Central Asia. East Asia (mainly China) is the centre of geographical distribution and diversity. So far only one fossil was found in Fushun, Liaoning province of China, which is indicative, but is not decisive for the place of origin. It is inferred that *Exochorda* originated in the temperate mountain zone of East Asia, the time of origin dates back to the Early Tertiary. It can be logically deduced that *Exochorda* originated before the emergence of the Taklamakan Desert. The genus probably once occupied a large area in the northern hemisphere of Asia. A formerly continuously distributed taxon became separated into different areas and has been subjected to divergent evolution there. The disjunction may represent the relict of a former wide and continuous distribution pattern, the intervening areas having been depopulated by the rigours of the climate.

Key words: Anatomy, biosystematics, cytology, distribution, embryology, *Exochorda*, morphology, multivariate analysis, pollination biology, populations, RAPD analysis, Rosaceae, taxonomy.

Samenvatting

Het genus *Exochorda* uit de rozenfamilie telde tot nu toe vijf geldig beschreven soorten en komt voor in Oost en Centraal Azië. Morfologisch hebben de taxa in het *Exochorda* complex overeenkomstige kenmerken, hetgeen problemen gaf met de classificatie in het complex. Een volgend probleem is de verwantschap tussen het genus *Exochorda* en andere genera in de Rosaceae. In dit proefschrift wordt een biosystematische studie gepresenteerd gebaseerd op wild materiaal van 22 in China verzamelde populaties, op gekweekte herkomsten in de Botanische Tuinen van de Landbouwuniversiteit Wageningen, en herbariummateriaal. De resultaten worden als volgt samengevat:

Bladanatomie: de epidermis bestaat uit één laag cellen en de vorm van de epidermiscellen is onregelmatig in omtrek aan beide zijden van het blad. De vorm van de epidermiscellen is tamelijk uniform in *Exochorda*. Stomata zijn alleen in het onderste bladoppervlak aanwezig. Alle monsters vertonen een anomocytisch patroon.

Houtanatomie: de groeiringen zijn te onderscheiden, de grenzen zijn kenbaar aan verschil in doorsnede tussen houtvaten gevormd in het voorjaar en de vorige zomer, en door rijen afgeplatte vezels gevormd in de zomer. Kwantitatieve anatomische kenmerken vertonen en continue reeks binnen de "soorten", de structuur van het hout van *Exochorda* is vergelijkbaar in alle onderzochte monsters, en gelijk aan dat van de Prunoideae en de Spiraeoideae.

Pollenmorfologie en de structuur van de exinelaag van de pollenkorrels vertonen weinig variatie binnen het genus. *Exochorda* stuifmeelkorrels zijn isopolair, drie-colporaat, klein of middelmatig van groote, en de vorm is rondachtig. P = 20.9-30.5 (19.6-36.9) µm, E = 22.1-30.7 (17.9-35.7) µm, A = 5.2-9.5 (3.6-15.5) µm, P/E = 0.88-1.36 (0.81-1.73). De oppervlakte is striaat/gestreept. Door de overeenkomst in deze kenmerken groeperen alle monsters dicht bij elkaar. Deze "soorten" moeten mede daarom tot één soort worden gerekend. Vergeleken met pollen van andere genera in Rosaceae, lijkt *Exochorda* pollen sterk op dat van *Neillia, Sorbaria, Spiraea* en *Prunus.*

Alle populaties zijn diploid (2n = 16 of 2n = 18), en deze aantallen zijn herhaaldelijk in eenzelfde worteltoppreparaat gevonden. De chromosomen zijn klein, 1-2 µm; er is weinig verschil tussen de chromosoomparen; de structuur is in principe metacentrisch; satellietchromosomen zijn niet waargenomen.

Het embryologisch onderzoek liet zien dat de meiose van de microsporenmoedercellen van het Simultane type zijn. Het tapetum van de helmhokken behoort tot het Glandular type.

Exochorda wordt gemengd bestoven, het is zowel een zelf-als een kruisbestuiver, en meer dan 7% van de nakomelingen zijn het resultaat van kruisbestuiving. De belangrijkste bestuivers zijn honingbijen, de grote aantallen die de bloemen bezoeken en het vlieggedrag van bloem tot bloem maken dat ze kwantitatief de grootste bijdrage leveren aan de reproductie van *Exochorda.* Meer dan 30 % van de stampers degenereren gedurende de

bloeiperiode, hetgeen ook een reden is van een lage vruchtzetting. De vruchtzetting varieert van 11% tot 70%.

Uit de resultaten van het RAPD-onderzoek bij sommige Rosaceae blijkt dat de vijf eerder onderscheiden taxa (soorten) van *Exochorda* niet duidelijk gescheiden kunnen worden, alle *Exochorda* monsters vallen binnen één groep en zijn verschillend van andere Rosaceae genera. De gegevens uit het moleculair onderzoek wijzen uit dat interspecifieke verwantschappen binnen *Exochorda* niet zo duidelijk zijn. De RAPD gegevens verstoren verder de algemene mening over de traditionele onderfamilies binnen de Rosaceae. In ieder geval zijn een paar van de vier onderfamilies als aparte taxonomische eenheden binnen de Rosaceae erg heterogeen.

De resultaten van de multivariate analyse laten een continue variatie zien van de morfologische kenmerktoestanden. Deze analyse ondersteunt de opvatting dat de verschillen in het algemeen klein zijn tussen de eenheden van het *Exochorda* complex. De multivariate analyse onderschrijft niet het bestaan van vijf verschillende taxa op soortsniveau, maar drie tamelijk zwak verschillende taxa kunnen worden onderscheiden. *E. korolkowii*, *E. tianschanica* en *E. racemosa* blijken geheel conspecifiek. *E. korolkowii* en *E. tianschanica* vervallen tot synoniemen van *E. racemosa*.

De gegevens uit eerdere hoofdstukken worden gebruikt in de taxonomische revisie van het genus om de taxa af te grenzen. De oorpronkelijke vijf verschillende "soorten" worden gereduceerd tot drie ondersoorten, met name *E. racemosa* (Lindl.) Rehder subsp. *racemosa*, subsp. *giraldii* (Hesse) F.Y. Gao & Maesen en subsp. *serratifolia* (S. Moore) F.Y. Gao & Maesen.

Het genus kan niet goed tot een van de vier klassieke onderfamilies in de Rosaceae worden gerekend. Classificatie in het tribus Exochordeae zonder onderfamiliestatus is passender.

Exochorda heeft een relatief nauwe en disjuncte verspreiding beperkt tot Oost en Centraal Azië. Oost Azië (vooral China) is het centrum van geografische verspreiding en diversiteit. Top op heden is in China slechts één fossiel gevonden in Fushun (Liaoning provincie). Dit is indicatief, maar niet beslissend om vast te stellen waar het oorsprongsgebied gelegen was. Er kan worden afgeleid dat de oorsprong van *Exochorda* gelegen is in het berggebied van Oost Azië met een gematigd klimaat, en daterend uit het Vroege Tertiair of het Palaeoceen. Het is logisch om te concluderen dat *Exochorda* ouder is dan de Taklamakan woestijn, die nu het areaal in twee ver uiteengelegen delen splitst. Het genus was voordien verspreid over een groot gebied in het aziatische deel van het noordelijk halfrond. Een eerder breed verspreid taxon raakte opgesplitst in verschillende gebieden en er vond gescheiden evolutie plaats. De disjunctie is het restant van een vroeger uitgebreid distributiepatroon, in de tussenliggende gebieden liet het klimaat overleving niet toe.

Trefwoorden: Anatomie, biosystematiek, cytologie, embryologie, *Exochorda*, morfologie, multivariate analyse, pollenmorfologie, populaties, RAPD analyse, Rosaceae, taxonomie, verspreiding.

摘要

蔷薇科白鹃梅属(*Exochorda*)有五个正式发表的种(邱园索引)，分布在东亚及西亚地区。形态上，该复合体有相似的特征，分类上存在着问题。另外该复合体与蔷薇科其他属之间的关系也存在着争议。本研究基于从中国采集的22个野外居群标本，荷兰瓦赫宁根农业大学植物园的栽培材料及标本室材料进行了生物系统学的研究，结果如下：

叶子解剖：叶表皮由一层细胞组成，表皮细胞形状不规则，细胞壁是直的或有些弯曲。表皮细胞形状的表面观单一，气孔限制在下表皮。气孔类型属anomocytic。

木材解剖的结果表明，生长年轮清楚，由大小不同的早材及晚材导管所区别。木材属环孔材或半环孔材。“种”间木材的数量解剖特征存在着连续变异。该复合体的木材显示单一的木材结构类型。

白鹃梅属的花粉形态及外壁结构显示较少的变化。花粉粒单极，三孔沟，小至中等大小，球形。P=20.9-30.5 (19.6-36.9) µm, E=22.1-30.7 (17.9-35.7) µm, A=5.2-9.5 (3.6-15.5) µm, P/E=0.88-1.36 (0.81-1.73). 外壁装饰为条形。由于花粉形态的相似性，所有的样品归为同种。与蔷薇科其他属的花粉形态比较，本属的花粉与*Neillia*, *Sorbaria*, *Spiraea*, 和 *Prunus* 属的更相似。

白鹃梅居群染色体均为二倍体(2n=16, 2n=18). 染色体小型，1-2µm，不同的染色体之间变化较小，中部着丝点，对称性高，没有随体。

胚胎学研究结果表明，小孢子母细胞的分裂为同时型，绒毡层属腺形。成熟胚囊为蓼形。

白鹃梅属有一个混合的繁育系统，自花授粉及异花授粉。大于7%的子代来源于自花授粉。最重要的传粉者为蜜蜂。它们相对较多的数量及花间形为，使它们成为白鹃梅属再生产成功的主要贡献者。开花期间，约30%以上的雌蕊不发育，这导致较低的结实率。结实率为11%至70%。

RAPD结果表明原来五个分类类群（五个种）没有明显的区别。所有的白鹃梅样品聚为一个组，而与蔷薇科其他属的样品分开。在白鹃梅复合体中RAPD结果没有显示明显的五个“种”的划分。这表明白鹃梅属中种间的关系不明显。RAPD结果也表明在传统的蔷薇科四个亚科中存在着很大的分化。至少四个亚科中的某些亚科有很强的异质性。

数量分类结果指出该复合体在形态特征上存在着连续的变化。形态特征的分析支持了在白鹃梅属中形态分化较小的观点。同样地，数量分类结果也没有支持本属五个类群的划分。然而，三个类群可以确定。*E. racemosa*, *E. korolkowii* 和 *E. tianschanica* 归为同种。*E. korolkowii* 和 *E. tianschanica* 作为 *E. racemosa* 的同名处理。综合研究结果用于该属的修改。即白鹃梅复合体为一个种。原先五个“种”合并为三个亚种，分别为：*E. racemosa* (Lindl.) Rehder subsp. *racemosa*, subsp. *giraldii* (Hesse) F.Y. Gao & Maesen 和 subsp. *serratifolia* (S. Moore) F.Y. Gao & Maesen.

该属不宜于以属的位置放在蔷薇科绣线菊亚科中。族的位置更合适。

白鹃梅属有一个相对窄的间断分布区，限于东亚及西亚。东亚(主要为中国)为其地理分布及多样性中心。迄今为止，在中国辽宁省抚顺发现了白鹃梅的叶化石。可以推测，该属起源于东亚的温带山区。起源时间推测为早第三纪。该属起源早于塔克拉玛干沙漠的形成，曾经占有亚洲北半球的广大地区。以前连续分布的一个类群变为现在间断分布的类群并进行分化。间断分布是

原来广阔的连续分布的孑遗，由于气候条件的变化，中间区域已经消失。

关键词：解剖，生物系统学，细胞学，分布，胚胎学，白鹃梅属，形态，数量分类，传粉生物学，居群，RAPD分析，蔷薇科，分类。

1. Introduction and history of the genus *Exochorda*

The Rosaceae are a large family of the angiosperms with about 124 genera and over 3300 species (Yu, 1977; Heywood, 1993). The family includes trees, shrubs and herbaceous plants, deciduous or evergreen with a worldwide distribution. The main development has taken place in temperate to subtropical regions in the northern hemisphere. Rosaceae are valued for many important tree fruits and popular horticultural ornamentals, as well as for timber and medicinal properties.

According to paleobotanical data, the Rosaceae originated in the Tertiary, many genera (i.e. *Crataegus, Malus, Rosa* and others) initiated from the late Eocene to the late Miocene (Takhtajan, 1963; Tao, 1992; Li, 1995).

Traditionally the Rosaceae have been treated as comprising four subfamilies, i.e. Spiraeoideae, Maloideae, Rosoideae and Prunoideae (Yu, 1977; Kalkman, 1988; Heywood, 1993). Sometimes the family is grouped into tribes (Bentham & Hooker, 1865; Hutchinson, 1964). In the present dissertation, four subfamilies are accepted.

Exochorda is a small genus of the Rosaceae. *Exo,* from Greek, means outside; *chorda*, cord, intestine, string. Lindley wrongly supposed, that the foeniculus of the seeds compared by him to an intestine or string (chord) was attached outside the carpel (Backer, 1936).

In 1846, during his first journey in China from 1843 to 1846, Robert Fortune, the British traveler and plant collector, collected a handsome shrub with long racemes of flowers near Ningpo, Zhejiang province, East China. He described it as a new species, *Amelanchier racemosa,* in his "Three Years Wandering in Northern Provinces of China" in October 1847. Lindley mentioned it in the Botanical Register Vol. 33 p. 38 in the same year, but a few months earlier, on July 1. At first view the species resembles a *Spiraea,* therefore William Jackson Hooker placed and figured this plant as *Spiraea grandiflora* in Botanical Magazine t. 4795 p. 439 in 1854. However, the differences with *Spiraea* are considerable, particularly in character of the fruits. *Exochorda* has lignified fruits and winged seeds, in *Spiraea* the fruits do not become woody and the seeds are without wings. Lindley proposed the new genus *Exochorda,* based on Hooker's *Spiraea grandiflora* in 1858 in Gard. Chron. p. 925. According to the principle of priority, Alfred Rehder made the necessary combination *Exochorda racemosa* in Sargent's Plantae Wilsonianae Vol. 1 p. 456 in 1913. The correct name is *Exochorda racemosa* (Lindl.) Rehder.

Exochorda is distributed in East Asia (mainly China) and Kirghizstan, Tadzhikistan, Turkestan and Uzbekistan; its species are cultivated in Europe and North America.

The genus *Exochorda* is unique within Rosaceae. It has 5 fused carpels, capsules and winged seeds. Traditionally it has been placed in the subfamily Spiraeoideae (Yu, 1977; Heywood, 1979). It is aberrant in any of the subfamilies (Challice, 1981). Some botanists prefer to place *Exochorda* in relation to *Prunus* (subfamily Prunoideae) (Goldblatt, 1976) or even to *Pyrus* (subfamily Maloideae) (Wallaart, 1980). According to Shu-Yin Zhang (1992), *Exochorda* is aberrant in Spiraeoideae and resembles Prunoideae in its wood anatomy. There is also confusion about the names and the number of species and varieties. Almost all the "species" are distinguished by the number of stamens, the size of the flower, the shape of the petals, the length of the petiole, the serration of the leaf margin, and the caducousness of the stipules. But in fact, all the aforementioned features are overlapping within the genus. None of these characters seem satisfactory or convincing. Some species were based on a single specimen, representing only the spring or autumn habit. The distinction between *E. korolkowii*, *E. tianschanica* and *E. racemosa* seems morphologically puzzling, because they show a high resemblance, especially in leaf shape.

In the Botanical Gardens of Wageningen Agricultural University, the Netherlands many *Exochorda* spp. obtained from nurseries as well as of wild origin have been planted. Particularly the cultivated plants are difficult to distinguish. When two shrubs of different species are grown side by side, the harvested seed can be of hybrid nature, and usually the cultivated plants are difficult to name. Among the plants of wild origin, there seem to be slight differences.

Some information on *Exochorda* could be found in epidermis morphology (Li Chaoluan, 1989; Li Gang, 1993), wood anatomy (Shu-yin Zhang, 1992), pollen morphology (Wang Fuhsiung, 1995), cytology (Sax, 1931 a; Goldblatt, 1976), microsporogenesis (Johnston, 1961; Van Heel, 1976), and one fossil record (Plant Fossils of China, Vol. III, 1978). The information on *Exochorda* from these resources is rather piecemeal. The taxonomy of *Exochorda* is problematical. In this dissertation we will focus on a comprehensive survey exploring the individual and phylogenetic development of *Exochorda*, with a combination of known data, to re-evaluate the systematics and phylogeny of this controversial genus and attempt to analyze the major evolutionary trends in the genus by comparison with other genera in Rosaceae. This regards morphology, particularly interspecific variation, and geographical distribution. This revision of *Exochorda* is also based on new collections of plants obtained from the wild.

In order to obtain wild materials, the author has traveled in the main areas where *Exochorda* occurs in China, including Jiansu, Zhejiang, Henan, Shaanxi, Shanxi, Hebei and Liaoning provinces and has surveyed 22 wild populations of *Exochorda* (Fig. 1.1). Hundreds of specimens were collected during 1994-1996. Table 1.2 gives some details of the 22 populations and their voucher specimens. Several populations were visited a second time (in spring and autumn). Two or more specimens were collected.

Other materials cultivated in the Beijing Botanical Garden, Chinese Academy of Science, and the Botanical Gardens of Wageningen Agricultural University were also studied (Table 1.1). Herbarium specimens were obtained on loan from a number of herbaria, which are mentioned in the acknowledgments.

In the early days of plant exploration in China, foreigners often had to invent their own spelling of place names, especially in little-known and previously unmapped areas.

In the early days of plant exploration in China, foreigners often had to invent their own spelling of place names, especially in little-known and previously unmapped areas. In English, the Wade-Giles spelling has been employed a long time. Eventually a system of romanisation, the post office system or Wade-Giles spelling was devised which covered the regions, provinces and all but the smallest towns. In many cases, the spelling of the place name was based on the local dialect, resulting in names like Amoy and Swatow.

In 1958, China began to popularise its own place name system known as Pinyin (spelt sound), and since 1979 this is the official system of transcribing Chinese names and places for publications in European languages printed in China.

I have used the Pinyin system in all but a few well-known names such as the Yangtze river. Where relevant, the Wade-Giles spelling has also been given in parentheses. Pinyin spellings in this book have been taken from the "Atlas of P. R. China" published in Beijing in 1995.

Table 1.1. Sources of *Exochorda* cultivated in WAU botanical gardens

Accession No.	Source
--BG22613	Deutschland, München, Germany
--BG23206	Middelburg, the Netherlands
--BG23207	Middelburg, the Netherlands
--BG23209	Middelburg, the Netherlands
--BG24230	Virginia, Boyce, U.S.A.
--BG24250	Ashkabad, Iran
84BG03409	Beijing, China
85BG35601	Frunze, Kirghizstan
85BGN0108	Boskoop, Esveld, the Netherlands
85BGN3204	Ochten, Tuincentrum & Kwekerij-Stam, the Netherlands
87BGN0113	Boskoop, the Netherlands
88BG16430	Vacratot, Hungary

Table 1.2. Origin of 22 populations of *Exochorda* collected in China

Pop.	Names in previous classification	Locality	Lat. & Long.	Alt. (m)	Habitat	Vouchers
01	*E. racemosa* (Lindl.) Rehder	Qixia Shan Mt., Nangjing, Jiangsu	32°09'N, 118°57'E	150	conifer-broad-leaved forest	Gao 0051
02	*E. racemosa* (Lindl.) Rehder	Chadaokou, Nangjing, Jiangsu	32°08'N, 118°56'E	100	bush grove	Gao 0052, 0053
03	*E. racemosa* (Lindl.) Rehder	Lingyan Shan Mt., Suzhou, Jiangsu	31°14'N, 120°30'E	145	bush grove	Gao 0056, 0057
04	*E. racemosa* (Lindl.) Rehder	Lingyan Shan Mt., Suzhou, Jiangsu	31°14'N, 120°30'E	70	coniferous forest	Gao 0062
05	*E. racemosa* (Lindl.) Rehder	Dengwei Shan Mt., Suzhou, Jiangsu	31°17'N, 120°23'E	195	bush grove	Gao 0063, 0103
06	*E. racemosa* (Lindl.) Rehder	Dengwei Shan Mt., Suzhou, Jiangsu	31°17'N, 120°23'E	150	bush grove	Gao 0064
07	*E. racemosa* (Lindl.) Rehder	Geling Mt., Hangzhou, Zhejiang	31°50'N, 114°00'E	150	conifer-broad-leaved forest	Gao 0065, 0090
08	*E. racemosa* (Lindl.) Rehder	Zhongtianmen, Jigong Shan Mt., Henan	31°50'N, 114°00'E	200	broad-leaved forest	Gao 0075
09	*E. racemosa* (Lindl.) Rehder	Baoxiaofeng, Jigong Shan Mt., Henan	31°50'N, 114°00'E	710	bush grove	Gao 0068, 0105, 0106
10	*E. racemosa* (Lindl.) Rehder	Longzikou, Jigong Shan Mt., Henan	31°50'N, 114°00'E	630	conifer-broad-leaved forest	Gao 0069, 0070
11	*E. racemosa* (Lindl.) Rehder	Longzikou to Doushiya, Jigong Shan Mt., Henan	31°50'N, 114°00'E	580	conifer-broad-leaved forest	Gao 0071, 0072, 0108
12	*E. racemosa* (Lindl.) Rehder	Doushiya, Jigong Shan Mt., Henan	31°50'N, 114°00'E	480	conifer-broad-leaved forest	Gao 0073
13	*E. racemosa* (Lindl.) Rehder	Xianrenjing, Jigong Shan Mt., Henan	31°50'N, 114°00'E	420	conifer-broad-leaved forest	Gao 0074
14	*E. racemosa* (Lindl.) Rehder	Entrance of Jigong Shan Mt., Henan	31°50'N, 114°00'E	110	deciduous broad-leaved forest	Gao 0076
15	*E. giraldii* Hesse	Heihuguan, Taibai Shan Mt., Shaanxi	34°00'N,107°43'E	1020	deciduous broad-leaved forest	Gao 0077, 0078, 0111
16	*E. giraldii* Hesse	Jiaokou, TaibaiShan Mt., Shaanxi	34°00'N, 107°43'E	1100	coniferous forest	Gao 0079, 0109
17	*E. giraldii* Hesse	Hua Shan Mt., Huayin, Shaanxi	34°27'N, 110°07'E	900	broad-leaved forest	Gao 0080
18	*E. giraldii* Hesse	Shigao Shan Mt., Lingshi, Shanxi	36°50'N, 111°46'E	1140	coniferous forest	Gao 0081, 0082, 0114
19	*E. serratifolia* S. Moore	Wuling Shan Mt., Xinglong, Hebei	40°30'N, 117°30'E	790	conifer-broad-leaved forest	Gao 0083, 0089
20	*E. serratifolia* S. Moore	Fenghuang Shan Mt., Chaoyang, Liaoning	41°34'N, 120°27'E	260	bush grove	Gao 0085, 0116, 0117
21	*E. serratifolia* S. Moore	Haitangshan Mt., Fuxin, Liaoning	42°03'N, 121°40'E	400	bush grove	Gao 0086, 0119, 0120
22	*E. serratifolia* S. Moore	Haitangshan Mt., Fuxin, Liaoning	42°03'N, 121°40'E	380	coniferous forest	Gao 0087

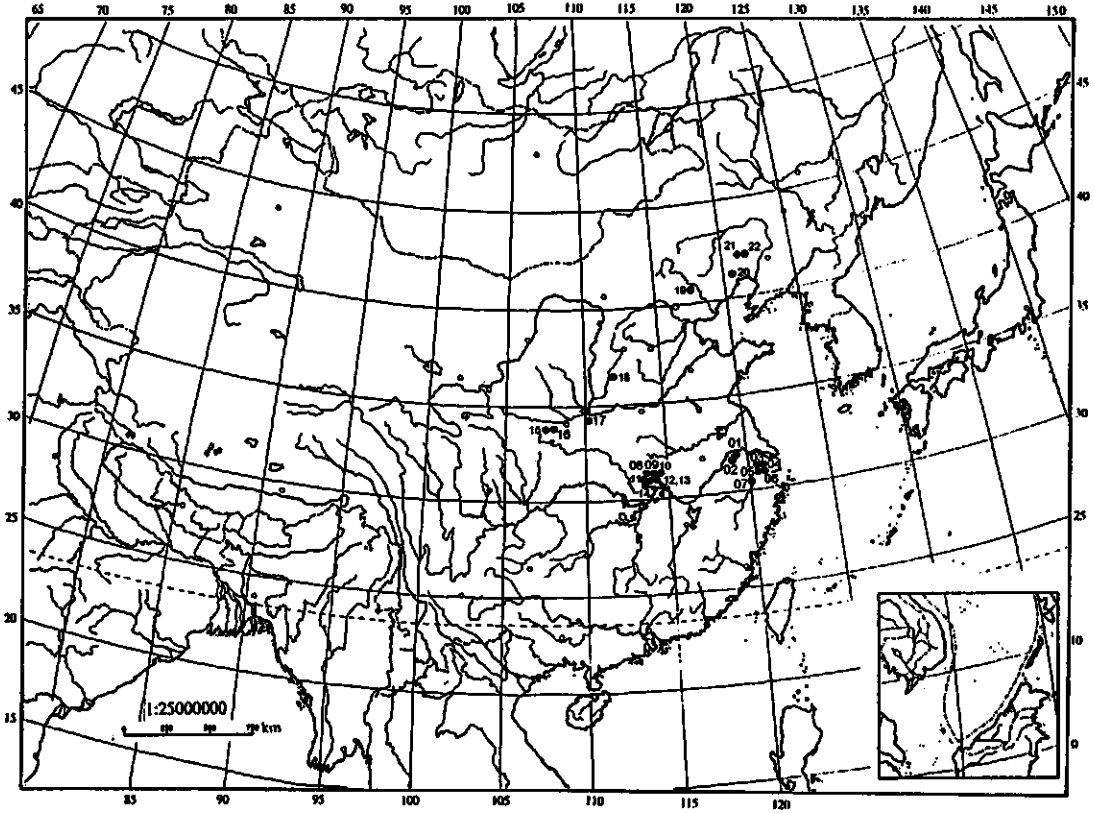

Figure 1.1. Distribution of 22 populations of *Exochorda* spp. collected from China. From Central Asia, herbarium material was seen.

2. Leaf morphology, anatomy and seedling morphology

2.1. Introduction

Investigation of morphology and anatomy of leaves has been carried out in a few taxa in Rosaceae. Jain & Singh (1975) and Singh & Jain (1975) studied the epidermal features of *Pyrus* and *Prunus*; Li Chaoluan (1989) emphasized the obvious systematic significance of stomatal types found in tribe Quillajeae of the subfamily Spiraeoideae; Li Gang (1993) carried out systematic and phylogenetic studies on Spiraeoideae. For its taxonomic importance (Metcalfe & Chalk, 1950; Stace, 1965; Van Cotthem, 1973; Wilkinson, 1979; Baranova, 1987), leaf epidermis and transverse sections of blade and petiole, and seedling morphology in *Exochorda* have been studied in this paper in order to obtain a better understanding of the generic limits and relationships with other genera in Rosaceae.

Classification of the seedlings of *Exochorda* has not been documented before. At present, seedling material is available for 3 "species" and an attempt is made to classify these.

2.2. Materials and methods

The experimental materials used for this study were taken from two sources: materials of wild origin: samples from native populations collected from China; and materials cultivated in the Botanical Gardens of Wageningen Agricultural University "Belmonte" and "De Dreijen". Voucher specimens are deposited in PE and WAG.

Mature leaves were macerated with boiling water for about 20 min. Epidermal peels taken from the middle portion between midrib and margin of leaves were extracted and bleached with hypochlorite, and mounted in glycerin.

Both dry and fresh material was used.

The characters of epidermal cells, stomatal types were observed under a light microscope (ZEISS) and photographs taken with a ZEISS Axiophot.

The transverse section of leaf blade and petiole anatomy were analyzed according to the method given by Arends & Van der Laan (1986) with some modifications. Leaf tissue was taken from the middle region of blades and fixed in a mixture of chromic acid, acetic acid and formalin mixture according to Navaschin (Sharma, 1972). After extraction and washing, materials were dehydrated in series of 0, 20, 30, 40, 50, 60, 70% solution of ethanol, 1 h for every concentration (70% ethanol for conservation). Materials were put into 96% ethanol for 3-4 h and 100% ethanol for >16 h. Pure ethanol was gradually replaced by Resin A (Resin A: 100 ml (or 25 ml) esin (Technovit 7100); 1 g (or 0.25 g) hardener I; 2.5 ml (or 0.625 ml) polyethylene glycol 400). Materials were imbedded in Resin B in small mould (stay 30 min) at 38 °C for 5 h (Resin B: 7 ml Resin A; 0.5 ml hardener II). The 6 µm sections of the leaf blade were made with a Leitz rotary microtome and dried on a heating table. They were stained with a 0.5% Toluidine Blue solution in 1N HCl, washed and left to dry. The slides were put into xylol and mounted in DPX.

The transverse sections of the leaf petiole were cut by hand, air was extracted and the sections were bleached in diluted household bleach, stained with safranine and mounted in glycerin.

The used terminology has been developed by Metcalfe & Chalk (1950) and Van Cotthem (1970).

Seed collections from different populations are shown in Table 2.1.

Seedlings are available of more than one population per "species". A general seedling description is given for each "species".

Table 2.1. Seed collections of different populations in China

Names in previous classification	Pop.	Locality	Alt. (m)	Vouchers
E. giraldii	15	Heihuguan, Taibai Shan Mt., Shaanxi	1020	Gao 0111
	18	Shigao Shan Mt., Lingshi, Shanxi	1140	Gao 0114, 0115
E. racemosa	03	Linyan Shan Mt., Suzhou, Jiangsu	145	Gao 0092
	05	Dewei Shan Mt., Suzhou, Jiangsu	195	Gao 0103
	09	Jigong Shan Mt., Henan	710	Gao 0107
E. serratifolia	19	Wuling Shan Mt., Xinglong, Hebei	790	Gao 0089
	20	Fenghuang Shan Mt., Chaoyang, Liaoning	260	Gao 0116, 0117, 0118
	21	Haitang Shan Mt., Fuxin, Liaoning	400	Gao 0120

2.3. Results

2.3.1. Leaf morphology

Mature leaves vary from long-elliptic to ovate or obovate, with mucronate, obtuse or acute apex and angustate or cuneate base. The margin varies from entire to serrate for 1/2 of its length at the top (see Chapter 10). The leaf size ranges from 3-9 cm long and 1.5-5 cm wide, the petiole is 0.5-2.5 cm long. Stipules are absent.

2.3.2. Epidermis morphology and stomatal type

Hairs: In *Exochorda*, hairs are long, thin-walled unicellular and non-glandular with an acute apex, caducous, erect (Plate II. 1). Only this type of hair was found. Hairs may be present on both the upper and lower epidermis, long, rather sparse (except Gao 0068 in population 09 which has dense hairs). The hair-base is inserted into the epidermis between the epidermis cells or replace a normal epidermis cell.

Epidermis: The epidermis is one layer of cells in thickness (Plate I. 1-6 & Plate II. 3, 4) and the shape of epidermis cells is irregular in outline as seen on both surface (Plate I. 1-6). In some samples, the wall of the epidermis cells is straight, or curved.

Stomata: Stomata are always confined to the lower leaf surface (Plate I. 5, 6). The stomatal distribution encountered in *Exochorda* is random. The terminology by Cotthem (1973) is used to describe the stomata. An anomocytic pattern is found in all samples. Stomata are surrounded by 6 irregular-cells that are indistinguishable in size and form from those of the remainder of the epidermis.

2.3.3. Transverse section of the leaf

The mesophyll consists of one layer of epidermis on both sides of the blade, two rows of palisade cells, spongy parenchyma and bundle sheaths and vascular bundles. The palisade tissue (cells narrowly oblong and length/width ratio more than 2) is more compact than the spongy tissue and located on the upper (adaxial, or "ventral") side of the blade. Such a structure is called bifacial or dorsiventral. The spongy parenchyma consists of cells of various shapes, irregular with branches extending from one cell to the other (Plate II. 3, 4).

The vascular bundle near the midrib is largest, bundles becoming smaller towards the margins (Plate II. 3).

The large vein is embedded in ground tissue that is not differentiated as mesophyll and has relatively few chloroplasts. The large vein is situated in the midrib that protrudes at the abaxial side of the blade.

The small vascular bundles located in the mesophyll are enclosed in one layer of compactly arranged cells forming the bundle sheath which is arranged on a horizontal axis from margin to margin in the leaf (Plate II. 3, 4). Xylem is orientated towards adaxial surface, interspersed with xylem-parenchyma. Phloem is not distinguishable from phloem-parenchyma. The bundle sheaths are connected with the epidermis by bundle sheath extensions that conduct water toward the epidermis (according to Esau, 1977) (Plate II. 4).

2.3.4. Petiole anatomy

The transverse sections through the distal end of the petiole exhibit a solitary crescent shape (similar to *Persea communis* Leone.) (Plate II. 2). A principal solitary crescent-shaped vascular bundle is accompanied by two smaller subsidiary vascular strands through the basal end. Calcium oxalate is present in the form of clustered crystals.

2.3.5. Seedling morphology

E. giraldii Hesse: Primary root well developed; Cotyledons green, glabrous, petiolate, rotundate with apex rounded, base truncate with two ears; first leaf rounded to obovate or subsequently rounded, apex obtuse and base cuneate, sparsely serrate above the middle, and sparsely hairs along the margin (Plate III. 1, 2).

The first leaf looks like a mature leaf, but has even more serrations.

E. racemosa (Lindl.) Rehder: Primary root well developed; Cotyledons green, glabrous, petiolate, rotundate, apex rounded and base truncate with two ears; first leaf elliptic, apex acute, base cuneate, margin serrate above 1/3 to 1/2 from the base, glabrous on both surfaces (Plate III. 3, 4).

The first leaf looks like a mature leaf.

E. serratifolia S. Moore: Primary root well developed; Cotyledons green, glabrous, petiolate, rotundate, apex rounded, base truncate with two ears; first leaf obovate, fiddle-shaped, apex rounded and base rounded, sparsely serrate from the middle to the top, brownish hairs along the margin (Plate III. 5, 6).

2.4. Discussion

The characters derived for the descriptions of the leaf anatomy provide systematic data for the genus.

The study indicates that epidermal cell shape in surface view is not very variable in *Exochorda*. This feature is very often identical in species groups or genera anyway. This feature can be scored as a character for one species .

This study also shows that the shape and size of the leaf is not of critical systematic value. This character is variable within and between many of the taxa studied, and size classes are difficult to establish due to continuous variation.

Although size and colour of the seedlings differ, this appears to be an indication of genotypical variation between populations rather than firm difference between species. The serration of the first leaf above the cotyledon is not restricted to *E. serratifolia* S. Moore.

Based on the morphological evidence, Li Gang (1993) pointed out that "*Exochorda* is aberrant in the Quillajeae," "all the cladograms treat this genus as a sister group for the Neillieae, Spiraeae and Gillenieae, transitional between Quillajeae and remaining Spiraeaoideae". My studies indicate that leaf shape and size are quite variable in Rosaceae. The absence of stipules is common in many Spiraeoideae. Leaf morphology has no importance on the generic level, but it is of rather weak importance in distinguishing *Exochorda* below the species level (see Chapter 9).

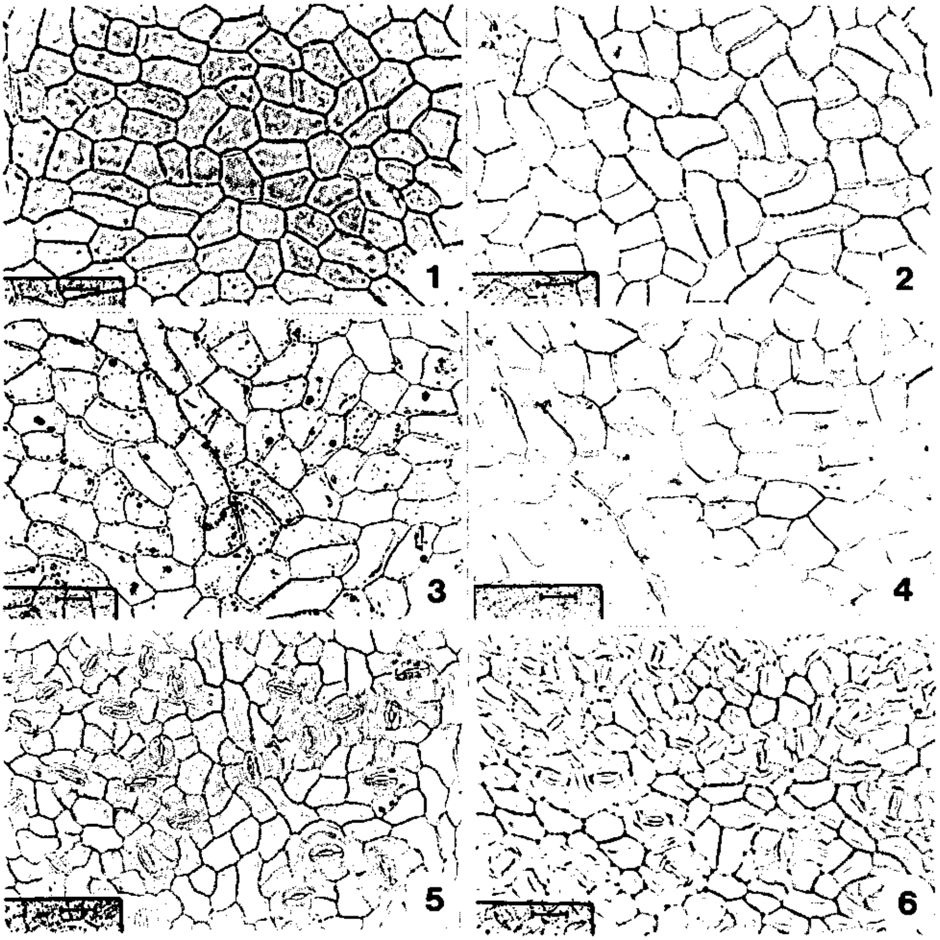

Plate I. 1-4. Epidermis cells of upper surface, showing straight or curved walls, samples 87BGN0113 (1), BG23209 (2), Gao 0076 (3), BG22675 (4). 5-6. Epidermis cells of lower surface, showing stomatal type, samples BG22613 (5), BG23209 (6). Bars = 31 μm.

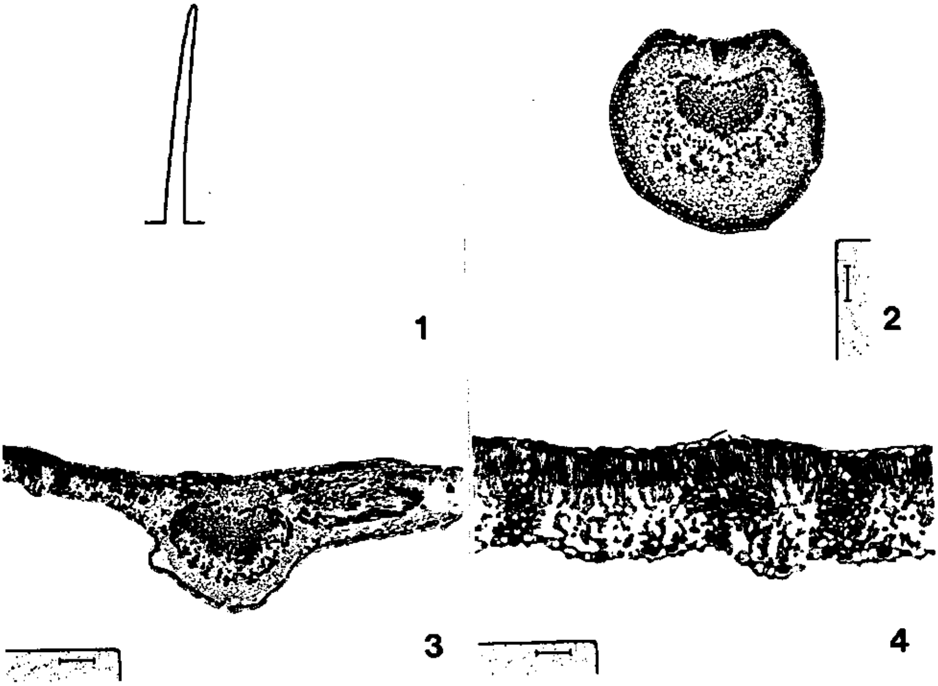

Plate II. 1. Hair type: unicellular non-glandular hairs; 2. Transverse section of petiole, sample BG23207, bar = 200 μm; 3. Transverse section of leaf blade, sample 85BG35601, bar = 200 μm; 4. Transverse section of leaf blade, sample BG23207, bar = 63 μm.

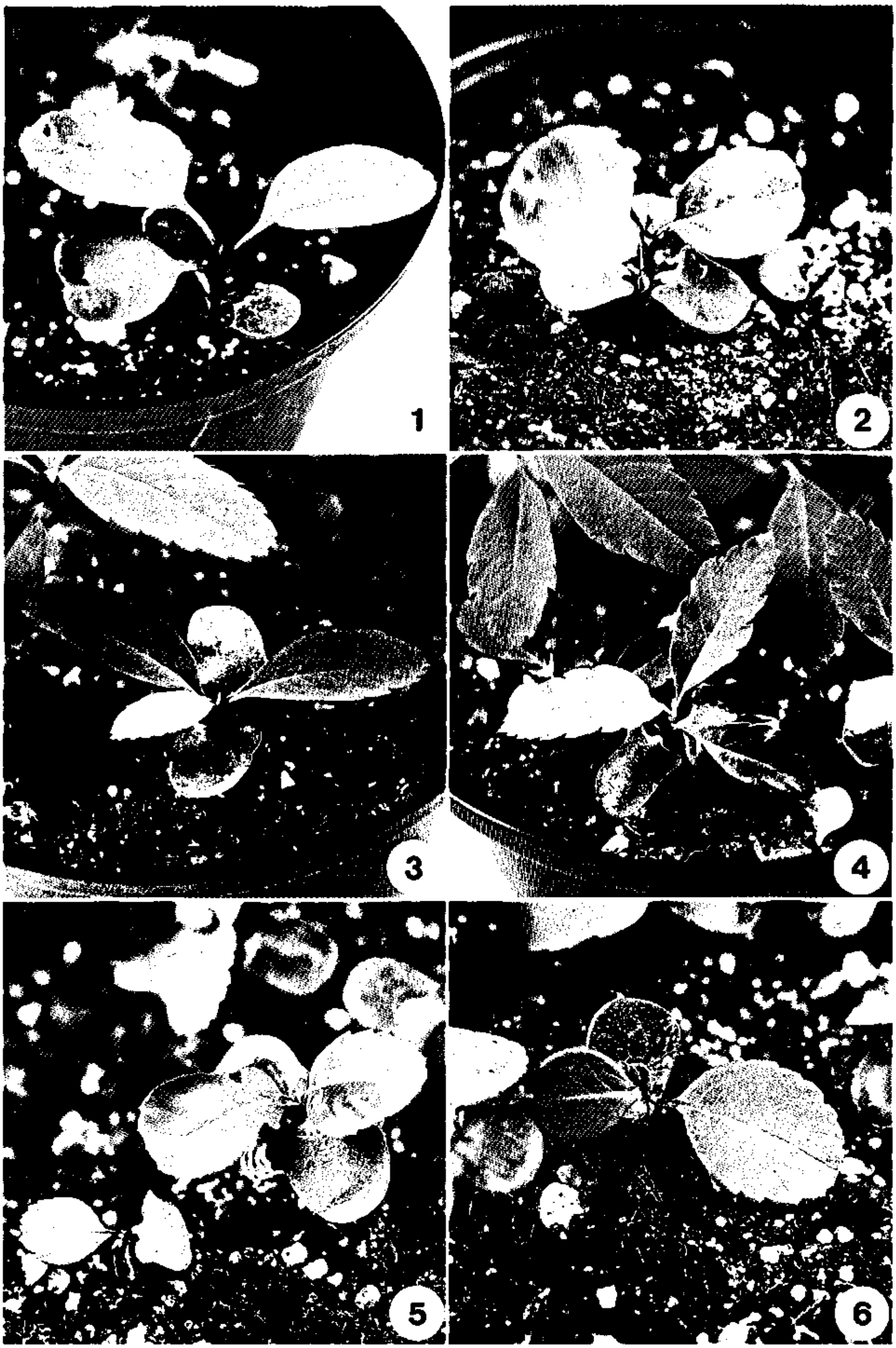

Plate III. Seedling morphology.
E. giraldii: Gao 0114 (1), Gao 0115 (2). *E. racemosa*: Gao 0092 (3), Gao 0103 (4).
E. serratifolia: Gao 0089 (5), Gao 0118 (6).

3. Wood anatomy

3.1. Introduction

Despite numerous earlier studies, the wood anatomy of the rich and diverse flora of China is still relatively poorly known. Publications by Tang (1932, 1933), Yu (1948, 1952), Cheng (1980, 1985), and others are very important contributions to the knowledge of wood structure of Chinese trees, but are often restricted to a limited region, to commercial species and to lens characters. The wood anatomy of Rosaceae from China was described and discussed in detail by Shu-yin Zhang & Baas in 1992. Only one species of *Exochorda, E. giraldii* Hesse, was studied by them.

The present study deals with *Exochorda*, a small genus which is indigenous to East Asia and Central Asia.

The wood anatomy of 30 samples belonging to some "species" of *Exochorda*, native in China and commonly cultivated in China and Wageningen Agricultural University, the Netherlands, is described in detail. The purpose of the chapter is to present a preliminary summary of wood data, gathered largely through investigation that are relevant to an understanding of the diversity of wood anatomy within the genus, to provide possibilities for the taxonomy of *Exochorda* and analyze ecological wood anatomy.

3.2. Materials and methods

Wood samples were obtained from the main areas of distribution in China and the Botanical Gardens "Belmonte" and "De Dreijen" of Wageningen Agricultural University (WAU). All samples were identified and conserved with flowering or fruiting parts. The voucher specimens are given in Table 3.1a, 1b.

The samples were boiled, sectioned for light microscope (LM) study in the usual way. Small blocks exposing transverse, radial and tangential sections were studied for LM. The terminology and measurements of quantitative features follow Baas & Zhang Xinying (1986).

Table 3.1a. Voucher specimens (names in previous classification)

Pop.	Names	Locality	Alt. (m)	MA*	Vouch.	Stem diam.(cm)
	E. racemosa	Cult. in Nanjing Forestry Univ.	150	N	Gao 0033	1.3
01	*E. racemosa*	Qixia Shan Mt., Nanjing, Jiangsu	150	N	Gao 0051	1.1
02	*E. racemosa*	Chadaokou, Nangjing, Jiangsu	100	N	Gao 0052	1.0
03	*E. racemosa*	Lingyan Shan Mt., Suzhou, Jiangsu	145	D	Gao 0056	1.0
03	*E. racemosa*	Lingyan Shan Mt., Suzhou, Jiangsu	95	D	Gao 0061	0.9
04	*E. racemosa*	Lingyan Shan Mt., Suzhou, Jiangsu	70	N	Gao 0062	1.3

05	*E. racemosa*	Dengwei Shan Mt., Suzhou, Jiangsu	195	D	Gao 0063	0.9
06	*E. racemosa*	Dengwei Shan Mt., Suzhou, Jiangsu	150	D	Gao 0064	0.7
07	*E. racemosa*	Geling Mt., Hangzhou, Zhejiang	150	N	Gao 0065	1.2
08	*E. racemosa*	Zhongtianmen, Jigong Shan Mt., Xinyang, Henan	200	N	Gao 0075	0.9
09	*E. racemosa*	Baoxiaofeng, Jigong Shan Mt., Henan	710	D	Gao 0068	1.1
10	*E. racemosa*	Longzikou, Jigong Shan Mt., Henan	630	N	Gao 0069	1.1
11	*E. racemosa*	Longzikou to Doushiya, Jigong Shan Mt., Henan	580	N	Gao 0071	1.2
12	*E. racemosa*	Doushiya, Jigong Shan Mt., Henan	480	N	Gao 0073	1.0
13	*E. racemosa*	Xianrenjing, Jigong Shan Mt., Henan	420	N	Gao 0074	1.0
14	*E. racemosa*	Entrance of Jigong Shan Mt., Henan	110	M	Gao 0076	0.8
15	*E. giraldii*	Heihuguan, Taibai Shan Mt., Shaanxi	1020	N	Gao 0077	1.5
16	*E. giraldii*	Jiaokou, Taibai Shan Mt., Shaanxi	1100	N	Gao 0079	1.4
17	*E. giraldii*	Huashan Mt., Shaanxi	900	M	Gao 0080	1.2
18	*E. giraldii*	Shigao Shan Mt., Lingshi, Shanxi	1140	D	Gao 0081	1.1
19	*E. serratifolia*	Wuling Shan Mt., Xinglong, Hebei	790	D	Gao 0083	1.1
20	*E. serratifolia*	Fenghuang Shan Mt., Chaoyang, Liaoning	260	D	Gao 0085	1.0
21	*E. serratifolia*	Haitang Shan Mt., Fuxin, Liaoning	400	D	Gao 0086	1.2
22	*E. serratifolia*	Haitang Shan Mt., Fuxin, Liaoning	380	D	Gao 0087	1.0
	E. serratifolia	Cult. in Shenyang, Liaoning		N	Gao 0136	0.9

MA*: moisture availability; N: normal; D: dry; M: mesic.

Table 3.1b.

No.*	Names in previous classification	Locality	Stem diam. (cm)
--BG23207	*E. giraldii*	WAU	1.8
--BG23209-a	*E. korolkowii*	WAU	2.0
87BGN0113	*E. x macrantha* 'The Bride'	WAU	1.6
--BG23206	*E. racemosa*	WAU	1.5
--BG24250	*E. tianschanica*	WAU	1.4

No*: accession number of collection in the Botanical Gardens of Wageningen Agricultural University.

3.3. Results

Generic wood anatomical description:

The following survey describes the range of variation in various wood anatomical features with diagnostic value in *Exochorda* of different populations. The wood anatomical description follows Wheeler et al. (1989).

Growth rings distinct, boundaries marked by differences in vessel diameter between earlywood and latewood, and by rows of flattened latewood fibres (Plate IV. 1).

Wood ring-porous to semi-porous, with 1-2 rows of large earlywood vessels. Latewood vessels 82-351/sq.mm, >90% solitary. Tangential diameter of earlywood vessels 32-56 (21-84) μm, radial diameter 35-61 (20-87) μm. Tangential diameter of latewood vessels 20-49 (12-67) μm, radial diameter 23-38 (13-51) μm. Vessel element length of latewood 148-249 (77-489) μm. Perforation plates exclusively simple in oblique end walls. Intervessel pits alternate (Plate IV. 4), nonvestured, oval or round, 4.3-7.0 (3.8-7.5) μm in diameter, with slit-like apertures. Helical thickenings well developed and closely spaced, mainly confined to narrow vessel elements. Fibres with distinctly bordered pits (Plate IV. 5).

Parenchyma common, apotracheally diffuse or scanty paratracheal.

Rays 8-13 (6-17)/mm, two sizes (Plate IV. 3): uniseriate rays and 2-5(6)-seriate rays. Uniseriate rays 10-17 (8-20) μm wide, 4-11 (2-26) cells and 89-199 (25-333) μm high, composed of square to weakly procumbent and upright marginal cells. Multiseriate rays 4-6 cells and 22-41 (9-72) μm wide, 15-29 (4-81) cells and 221-483 (103-1450) μm high, composed of procumbent body cells and 1-5 rows of square to upright marginal cells.

Crystals common, prismatic, in procumbent and square cells (Plate IV. 6).

Selected wood anatomical characters for individual samples are listed in Table 3.2a, 2b, 2c.

Table 3.2a. Variation in selected wood anatomical features of *Exochorda* spp.*

Pop.	Coll. No.	1	2	3	4	5	6	7	8
	Gao 0033	+	1-2	82	>90	41(56)72	41(56)72	21(29)41	21(33)46
01	Gao 0051	+	1	174	>90	41(52)62	46(60)77	26(33)46	26(38)51
02	Gao 0052	+	1	195	>90	36(45)72	41(48)72	26(31)36	31(35)41
03	Gao 0056	+	1	201	>90	30(44)56	31(46)56	26(31)36	26(35)41
03	Gao 0061	+	1	208	>90	36(53)72	46(59)77	21(31)41	21(33)41
04	Gao 0062	+	1	250	>90	41(50)72	46(61)87	26(32)41	26(35)41
05	Gao 0063	+	1	198	>90	31(45)56	41(52)62	26(28)36	26(32)41
06	Gao 0064	+	1	156	>90	31(41)56	36(44)56	26(29)31	26(30)41
07	Gao 0065	+	1	175	>90	31(45)67	36(51)72	26(33)41	31(38)46
08	Gao 0075	+	1-2	189	>90	36(51)62	36(54)72	26(32)36	31(37)41
09	Gao 0068	+	1	300	>90	31(42)51	47(36)62	21(25)31	21(27)31

10	Gao 0069	+	1	335	>90	31(45)62	36(49)67	36(49)67	26(32)41
11	Gao 0071	+	1-2	207	>90	41(52)72	41(58)72	26(27)31	26(30)36
12	Gao 0073	+	1-2	269	>90	36(45)56	36(52)72	26(30)36	26(35)41
13	Gao 0074	+	1-2	220	>90	36(46)56	41(50)67	26(31)36	26(37)46
14	Gao 0076	+	1-2	328	>90	41(44)56	41(48)56	26(28)36	26(28)36
15	Gao 0077	+	1	193	>90	31(46)56	31(49)67	21(29)36	21(35)41
16	Gao 0079	+	1	284	>90	31(43)56	36(47)62	21(25)31	21(27)31
17	Gao 0080	+	1-2	351	>90	31(53)72	41(49)72	21(29)36	26(32)41
18	Gao 0081	+	1	226	>90	36(47)56	41(59)77	26(28)31	26(31)36
19	Gao 0083	+	1	290	>95	36(47)67	36(53)77	21(29)36	21(30)36
20	Gao 0085	+	1	320	>95	31(46)56	31(50)56	21(23)31	21(23)31
21	Gao 0086	+	1	266	>95	36(49)67	36(51)72	21(26)31	21(28)36
22	Gao 0087	+	1	331	>95	36(49)72	41(56)77	21(24)31	21(27)31
	Gao 0136	+	1	300	>95	36(46)56	36(50)67	21(29)36	21(30)36
	--BG23207	+	1-2	189	>99	24(34)51	30(43)55	30(43)55	13(25)33
	--BG23209-a	+	1-2	114	>99	21(48)84	30(58)84	12(20)30	18(24)36
	87BGN0113	+	1-2	173	>99	27(34)43	30(40)51	18(26)36	18(26)36
	--BG23206	+	1-2	130	>99	30(49)69	30(49)69	15(23)33	18(27)36
	--BG24250	+	1-2	242	>99	21(32)45	20(35)42	15(23)30	17(27)30

*: The legends are given at the end of the tables.

Table 3.2b.

Pop.	Coll. No.	9	10	11	12	13	14
	Gao 0033	103(167)287	5.4	5.0(5.5)6.3	7(9)12	4	15(32)41
01	Gao 0051	113(186)241	5.2	5.0(5.5)6.3	8(10)13	4	21(37)56
02	Gao 0052	108(186)374	5.6	3.8(4.8)5.0	8(9)10	5	21(41)67
03	Gao 0056	103(157)231	4.8	5.0(5.5)6.3	8(9)11	4	21(34)46
03	Gao 0061	133(162)215	5.1	6.3(6.4)6.9	7(9)10	4	31(39)51
04	Gao 0062	154(213)436	6.4	5.0(5.5)6.3	8(10)13	4	26(37)51
05	Gao 0063	77(161)231	5.4	5.0(5.3)6.3	8(11)14	4	9(22)51
06	Gao 0064	92(159)221	5.4	5.0(5.3)6.3	7(10)13	4	26(40)72
07	Gao 0065	128(196)256	5.5	3.8(5.0)6.3	9(11)13	4	21(32)36
08	Gao 0075	128(201)282	5.8	5.0(6.0)7.5	8(10)12	4	26(30)41
09	Gao 0068	82(148)205	5.7	5.0(5.1)5.6	8(10)13	4	21(41)51
10	Gao 0069	113(158)179	3.9	5.0(6.0)7.5	9(11)13	4	26(35)46
11	Gao 0071	103(148)221	6.4	5.6(6.0)6.3	7(9)12	4	21(35)51
12	Gao 0073	113(181)231	5.6	6.3(7.0)7.5	8(10)13	4	26(33)41
13	Gao 0074	103(194)282	5.7	5.0(6.0)6.3	7(9)11	4	26(31)41
14	Gao 0076	87(175)241	6.3	5.0(6.0)7.5	8(11)14	4	31(38)62
15	Gao 0077	92(178)333	5.6	4.4(4.8)5.0	9(12)14	4	21(40)62
16	Gao 0079	103(155)205	6.0	5.0(6.0)7.5	7(9)11	4	21(33)41
17	Gao 0080	128(211)308	6.9	5.0(6.0)7.5	7(10)13	5	15(34)51
18	Gao 0081	82(149)205	5.1	5.0(4.9)5.6	7(11)13	6	21(39)62
19	Gao 0083	77(164)267	5.6	5.0(5.0)5.0	8(10)14	4	21(36)51

20	Gao 0085	92(156)205	6.8	4.4(5.1)6.3	8(10)11	4	26(38)51
21	Gao 0086	118(151)205	5.6	4.4(5.6)7.5	9(11)13	4	21(29)36
22	Gao 0087	113(163)205	6.4	5.6(6.1)6.3	8(11)14	4	21(29)41
	Gao 0136	118(154)190	5.2	5.0(5.6)6.3	9(10)11	5	26(40)62
	--BG23207	111(199)303	5.9	5.0(5.8)6.3	10(13)14	5	20(38)60
	--BG23209-a	93(171)231	7.8	3.8(4.6)5.0	8(10)11	4	25(36)50
	87BGN0113	159(249)489	9.6	3.8(4.5)5.0	10(12)14	5	25(34)60
	--BG23206	111(190)297	7.6	3.8(5.3)7.5	6(8)10	5	15(38)60
	--BG24250	108(169)234	6.8	3.8(4.3)5.0	11(13)17	4	20(33)40

Table 3.2c.

Pop.	Coll. No.	15	16	17	18	19	20
	Gao 0033	8(20)42	118(279)564	10(11)15	4(6)8	62(105)133	+
01	Gao 0051	10(24)55	174(410)667	10(12)15	4(8)12	159(173)256	+
02	Gao 0052	11(21)44	164(344)744	8(10)10	4(6)8	103(111)128	+
03	Gao 0056	8(24)47	205(483)913	10(12)15	4(7)12	182(160)256	+
03	Gao 0061	9(16)33	169(249)513	10(13)15	4(6)11	62(118)205	+
04	Gao 0062	9(21)44	128(393)475	10(12)15	3(6)8	77(142)190	+
05	Gao 0063	14(21)32	185(366)574	10(10)10	4(7)10	62(162)256	+
06	Gao 0064	9(22)51	169(374)795	10(11)15	3(7)13	77(165)205	+
07	Gao 0065	8(26)65	154(401)974	10(11)15	3(11)26	62(126)205	+
08	Gao 0075	11(23)38	179(410)692	10(13)15	3(7)16	56(175)256	+
09	Gao 0068	8(23)43	118(407)769	10(12)15	7(8)10	113(199)282	+
10	Gao 0069	9(21)37	195(363)667	10(13)15	6(8)9	103(157)205	+
11	Gao 0071	9(19)35	169(317)564	10(10)10	2(6)9	31(99)154	+
12	Gao 0073	9(19)32	164(309)513	10(12)15	3(5)7	67(107)144	+
13	Gao 0074	17(24)36	205(448)769	10(10)10	7(9)17	138(190)333	+
14	Gao 0076	8(20)30	154(317)513	10(11)15	5(8)13	103(156)205	+
15	Gao 0077	7(21)36	128(341)538	10(11)15	5(7)9	92(113)164	+
16	Gao 0079	6(18)51	103(283)785	10(11)15	2(6)12	51(125)231	+
17	Gao 0080	5(18)30	128(276)492	10(11)15	4(5)8	103(118)154	+
18	Gao 0081	6(17)47	128(343)733	10(11)15	2(5)9	67(125)271	+
19	Gao 0083	6(15)25	103(221)369	10(11)15	2(5)8	67(125)271	+
20	Gao 0085	6(16)26	103(229)410	10(12)15	3(5)7	51(95)144	+
21	Gao 0086	8(20)36	118(275)472	10(12)15	3(6)9	51(116)179	+
22	Gao 0087	11(16)32	154(223)441	10(10)10	3(6)10	51(89)154	+
	Gao 0136	8(20)35	144(334)651	10(12)15	2(5)9	41(112)231	+
	--BG23207	4(23)81	130(456)1450	10(12)13	3(6)8	25(102)200	?
	BG23209-a	4(25)50	120(293)500	10(13)15	2(6)9	50(117)220	?
	87BGN0113	7(29)52	200(395)825	10(16)20	2(4)7	50(113)220	?
	--BG23206	6(26)56	115(245)440	10(12)15	2(5)9	90(115)175	?
	--BG24250	8(26)64	150(459)1150	13(17)20	2(6)12	35(103)160	?

Legends to Table 3.2:

1. Growth ring: present(+), or absent(-).
2. Ring-porosity: 1 = ring-porous; 2 = semi-ring-porous; 3 = diffuse-porous.
3. Vessel frequency (number/sq. mm), grouping shape: number per square mm, was determined by counting all vessels individually (as opposed to counting each multiple as a single pore).
4. Percentage of solitary vessels (%): the proportion of solitary vessels in relation to the total number of vessels (cf. Wheeler, 1986).
5. Tangential vessel diameter of earlywood (µm) (min., average, and max.), including the walls, was measured of 20 vessels of each specimen.
6. Radial vessel diameter of earlywood (µm) (min., average, and max.), was measured of 20 vessels of each specimen.
7. Tangential vessel diameter of latewood (µm) (min., average, and max.), was measured of 20 vessels of each specimen.
8. Radial vessel diameter of latewood (µm). (min., average, and max.), was measured of 20 vessels of each specimen.
9. Vessel member length (of latewood) (µm) (min., average, and max.) including tails based on 20 measurements.
10. L/D ratio (of latewood) [= 9/(7+8)/2].

    The ratio of vessel element length/vessel diameter (L/D ratio) is used as an index of vessel element shape.
11. Size of intervessel pits (µm) (min., average, and max.) is based on 5 measurements.
12. Ray frequency (number/mm) (min., average, and max.) was determined in transverse sections, counting the number of rays intersecting a tangential line of 1 mm (20 counts per sample).
13. Multiseriate ray width (number of cells).
14. Multiseriate ray width (µm) (min., average, and max.).
15. Multiseriate ray height (number of cells) (min., average, and max.).
16. Multiseriate ray height (µm) (min., average, and max.).
17. Uniseriate ray width (µm) (min., average, and max.).
18. Uniseriate ray height (number of cells) (min., average, and max.).
19. Uniseriate ray height (µm) (min., average, and max.).

    Ray size was expressed in number of cells (width and height) as well as µm for width and height. Ray type was classified according to Kribs (1950, 1968).
20. Prismatic crystal in ray cells (+), or absent (-).

3.4. Discussion and conclusions

3.4.1. Species delimitation and relationship with other genera in Rosaceae

The number of specimens studied is relatively large and sufficient to eliminate variation among different populations within the genus.

Quantitative characters express continuous variation within the "species", but the wood of *Exochorda* shows a single wood structural type similar to that of the Prunoideae than to the Spiraeoideae.

Prismatic crystals exist in all samples of wild material.

The study of wood does not provide a useful delimitation of the "species", but it does support the relationship with other genera in Rosaceae. According to Shu-yin Zhang (1992), "Wood anatomically *Exochorda* is aberrant in the Spiraeoideae. The genus is more similar to the Prunoideae than to the Spiraeoideae". "However, the percentage of solitary vessels in the genus is higher than in the Prunoideae". Our observations concur with his findings, confirming the peculiar separate place of the genus in the constellation of subfamilies of Rosaceae.

Wood anatomy is similar for the various populations, hence not of importance for taxonomy at the species level. Temperature and moisture influence the size of the elements, being large in subtropical regions, and more numerous in temperate or moist conditions. In dry regions, semi-ring porosity is absent.

3.4.2. Ecological trends in wood of *Exochorda* in China

To put the *Exochorda* data in perspective, diagrams are given for vessel frequency, vessel member length, vessel diameter etc (Figs. 3.1-6). Vessel diameter and frequency are crucial parameters for hydraulic conductivity of wood (Zhang Xinying, 1986).

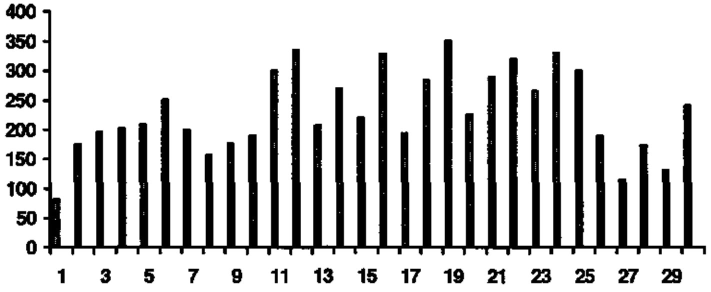

Figure 3.1. Vessel frequency (number/sq. mm). X: populations; Y: vessel frequency (number/sq. mm).

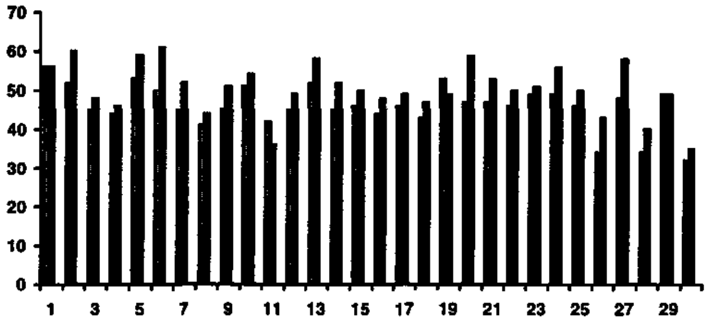

Figure 3.2. Tangential and radial vessel diameter (µm) of earlywood. gray = tangential vessel diameter (µm) of earlywood; black = radial vessel diameter (µm) of earlywood; X: populations; Y: vessel diameter (µm).

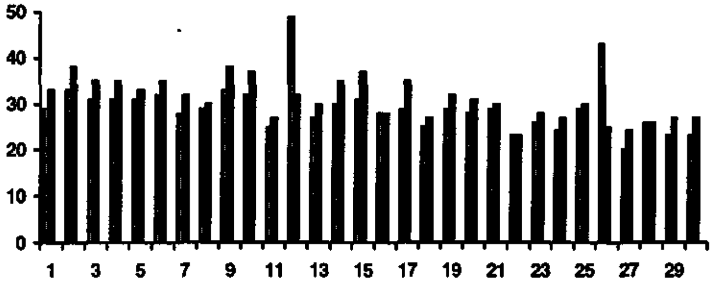

Figure 3.3. Tangential and radial vessel diameter (µm) of latewood. gray = tangential vessel diameter (µm) of latewood; black = radial vessel; diameter (µm) of latewood; X: populations; Y: vessel diameter (µm).

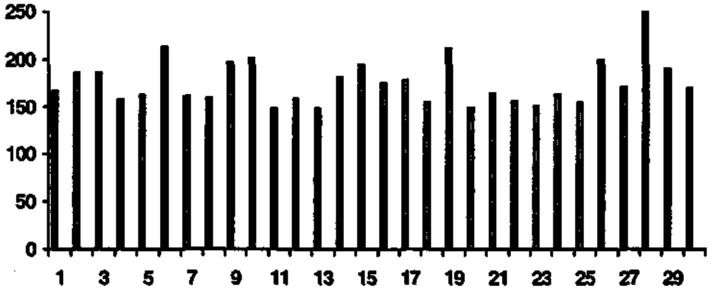

Figure 3.4. Vessel member length (µm). X: populations; Y: vessel member length (µm).

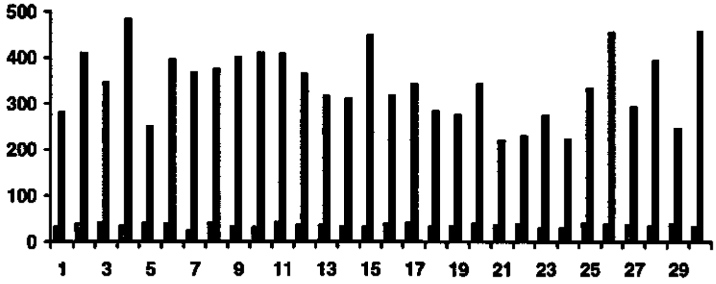

Figure 3.5. Multiseriate ray width (μm) and multiseriate ray height (μm). gray = multiseriate ray width (μm); black = multiseriate ray height (μm); X: populations; Y: μm.

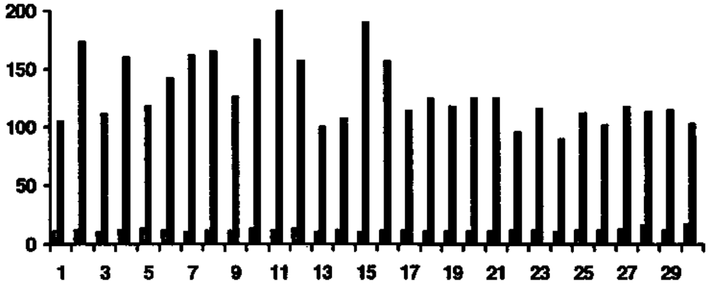

Figure 3.6. Uniseriate ray width (μm) and uniseriate ray height (μm). gray = uniseriate ray width (μm); black = uniseriate ray height (μm); X: populations; Y: μm.

Exochorda covers a relatively narrow range of habitats, including temperate and subtropical forests. Its phenological variation and habits are limited to deciduous and shrub vegetation.

The present study has ecological data for samples in China. Necessary ecological date are altitude, and moisture availability. For the purpose of study, the following broad ecological categories were recognized.

Macroclimate zones: 1. Subtropical sample (occurring between 23°30' N and 32°00' N); 2. Temperate sample (occurring north of 32°00' N). For *Exochorda* native to China, all samples belong to subtropical or temperate species. This classification ignores vast altitudinal variation within each region.

Moisture availability: Very rough and arbitrary categories were adopted. 1. Dry: samples from physically and/or physiologically dry habitats; 2. Mesic: samples from relatively moist habitats; 3. Normal: samples from habitats intermediate in moisture availability between the two above categories.

3.4.2.1. Mutual relationship between macroclimate and moisture availability

Mutual relationship between macroclimate and moisture availability is depicted in Fig. 3.7. The percentage of the *Exochorda* populations sampled by the author in China subjected to dry conditions gradually increases from subtropical to temperate regions, while the percentage of normal condition decreases.

3.4.2.2. Wood anatomical characters in relationship to ecology

Ring-porosity: Ring-porosity decreases from temperate to subtropical regions, while semi-ring-porosity increases (Fig. 3.8). This proves that the incidence of ring-porosity in temperate regions is more common than in the subtropics (e.g. Baas et al., 1983; Wheeler & Baas, 1991). It also coincides with the findings for Rosaceae in general (cf. Shu-yin Zhang, 1992). The *Exochorda* wood samples are predominantly ring-porous. With decreasing moisture availability, ring-porosity increases, the percentage of semi-ring-porous is zero under dry conditions (Fig. 3.9).

Vessel frequency: Vessel frequency decreases from temperate to subtropical regions (Fig. 3.10). With increasing moisture availability, vessel frequency increases (Fig. 3.11), in contrast with the finding for *Exochorda* (cf. Shu-yin Zhang, 1992). Vessel frequency shows little variation between normal and dry conditions.

Percentage of solitary vessels: Macroclimate and moisture availability do affect the percentage of solitary vessels. It is noticed that the percentage of the samples with almost only solitary vessels (>95%) in temperate zones is much higher than in subtropical areas (Table 3.2a).

Vessel diameter: Tangential and radial vessel diameter (of earlywood and latewood) tends to increase from temperate to subtropical regions (Figs. 3.12-15). It tends to decrease relatively with decreasing moisture (but relatively mesic conditions produce an intermediate diameter) (Figs. 3.16-17).

Vessel element length: Vessel element length tends to increase from temperate to subtropical regions (Fig. 3.18). Vessel element length also increases with increasing moisture availability (Fig. 3.19). The variation of vessel element length with ecology (macroclimate and moisture availability) conforms to general trends (Baas 1976, 1982, 1986; Carlquist & Hoekman, 1985; Carlquist, 1988; Shu-yin Zhang, 1992).

Ray width: Ray width tends to increase from temperate to subtropical regions (Fig. 3.20). There is little relationship between ray width and moisture (Fig. 3.21).

Ray height: Ray height tends to increase from temperate to subtropical regions (Fig. 3.22). Ray height also tends to increase with decreasing moisture availability. This is not in agreement with general trends in Rosaceae (Shu-yin Zhang, 1992).

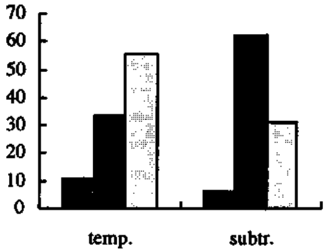

Figure 3.7. Macroclimate and moisture availability. temp.= temperate; subtr.= subtropics; gray = mesic; black = normal; white = dry; Y: percentage.

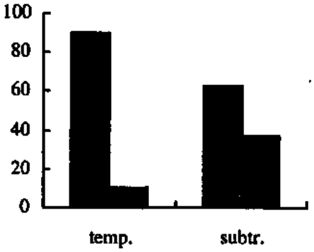

Figure 3.8. Macroclimate and ring-porosity temp.= temperate; subtr.= subtropics; gray = ring-porous; black = semi-ring-porous; Y: percentage.

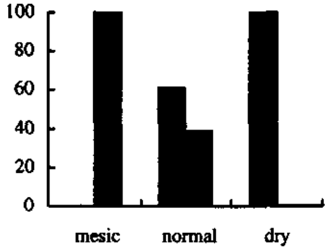

Figure 3.9. Moisture availability and ring-porosity. black = semi-ring-porous; gray = ring-porous; Y: percentage.

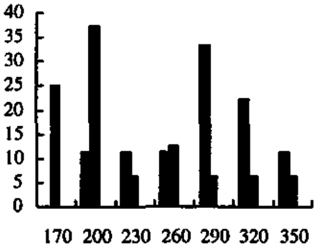

Figure 3.10. Macroclimate and vessel frequency. gray = ring-porous; black = semi-ring-porous; X: vessel frequency (number/sq. mm); Y: percentage.

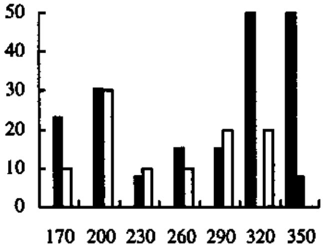

Figure 3.11. Moisture availability and vessel frequency. black = normal; gray = mesic; white = dry; X: vessel frequency (number/sq. mm); Y: percentage.

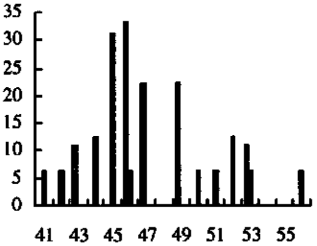

Figure 3.12. Macroclimate and tangential vessel diameter of early wood. gray = temperate; black = subtropical; X: µm; Y: percentage.

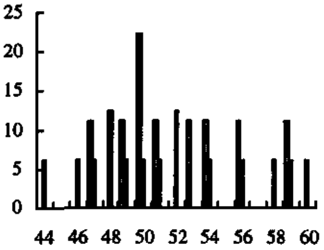

Figure 3.13. Macroclimate and radial vessel diameter of early wood. gray = temperate; black = subtropical; X: µm; Y: percentage.

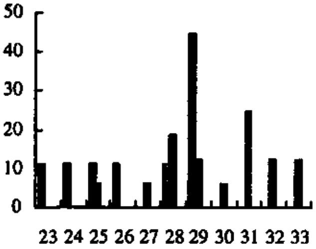

Figure 3.14. Macroclimate and tangential vessel diameter of late wood. gray = temperate; black = subtropical; X: µm; Y: percentage.

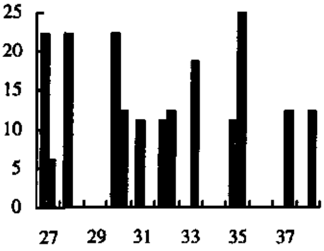

Figure 3.15. Macroclimate and radial vessel diameter of late wood. gray = temperate; black = subtropical; X: µm; Y: percentage.

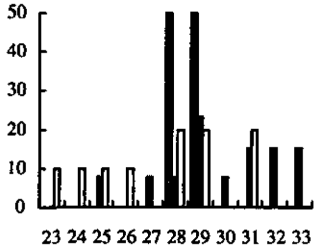

Figure 3.16. Moisture availability and tangential vessel diameter of late wood. gray = mesic; black = normal; white = dry; X: µm; Y: percentage.

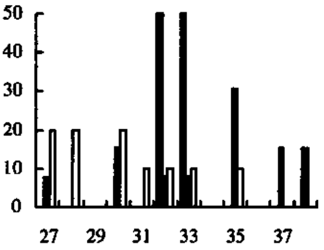

Figure 3.17. Moisture availability and radial vessel diameter of late wood. gray = mesic; black = normal; white = dry; X: µm; Y: percentage.

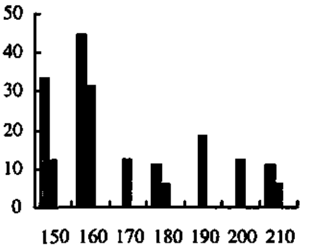

Figure 3.18. Macroclimate and vessel element length. gray = temperate; black = subtropical; X: µm; Y: percentage.

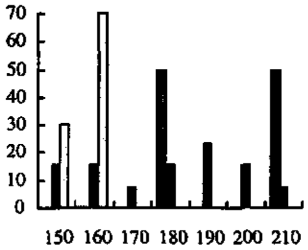

Figure 3.19. Moisture availability and vessel element length. gray = mesic; black = normal; white = dry; X: µm; Y: percentage.

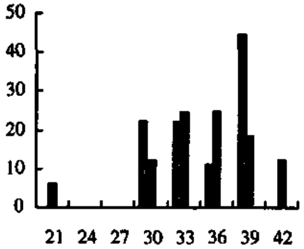

Figure 3.20. Macroclimate and ray width. gray = temperate; black = subtropical; X: µm; Y: percentage.

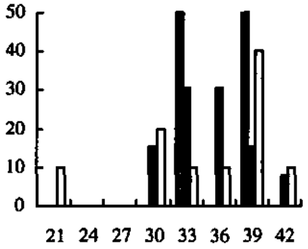

Figure 3.21. Moisture availability and ray width. gray = mesic; black = normal; white = dry; X: µm; Y: percentage.

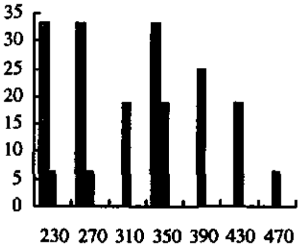

Figure 3.22. Macroclimate and ray height. gray = temperate; black = subtropical; X: µm; Y: percentage.

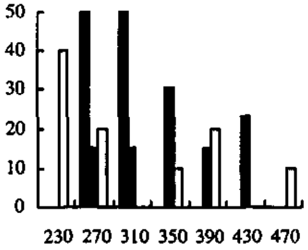

Figure 3.23. Moisture availability and ray height. gray = mesic; black = normal; white = dry; X: µm; Y: percentage.

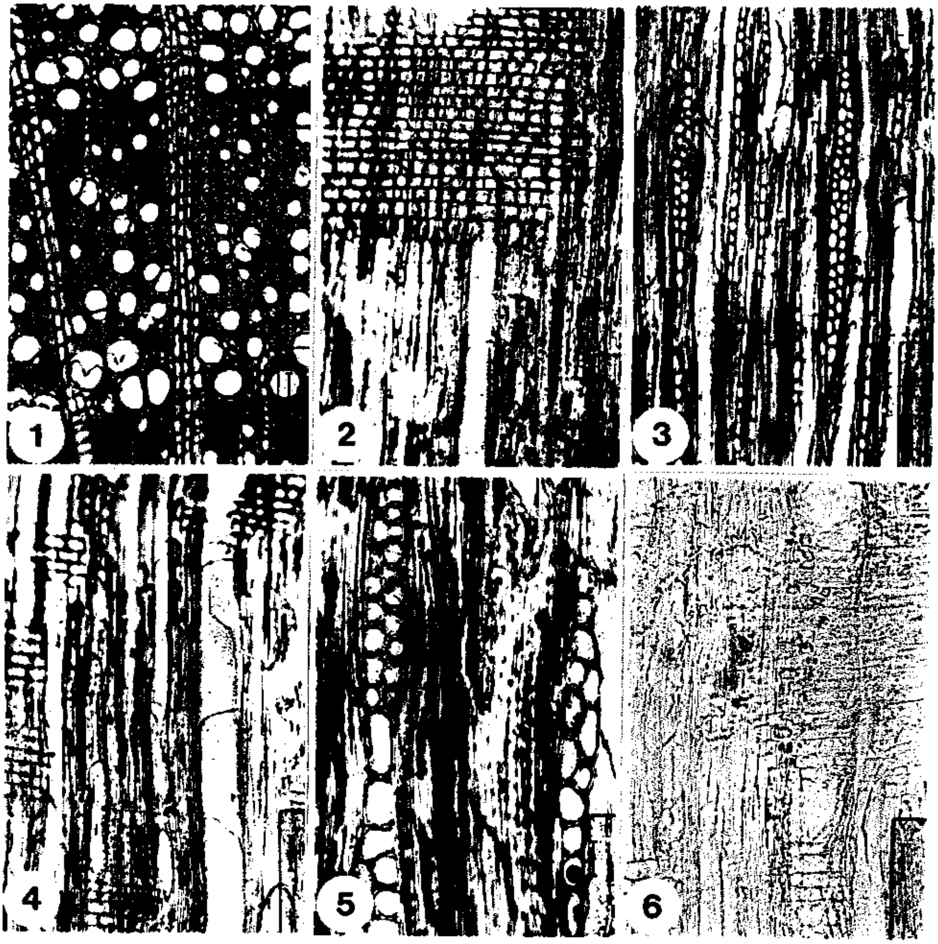

Plate IV. 1. Transverse section, Pop. 03, bar = 49 µm; 2. Radial section, Pop. 02, bar = 49 µm; 3. Tangential section, Pop. 03, bar = 49 µm; 4. Intervessel pits alternate, Pop. 21, bar = 49 µm; 5. Fibres with distinctly bordered pits, Pop. 12, bar = 21 µm; 6. Crystal, Pop. 17, bar = 40 µm.

4. Pollen morphology

4.1. Introduction

Pollen of *Exochorda racemosa* (Lindl.) Rehder has already been described with light microscopy (LM) by Wang Fuhsiung (1995), and pollen shape, size measurements, photographs and brief description of the surface sculpturing were provided. The present study differs from previous reports in that: 1. for the first time, the ultrastructure of pollen of *Exochorda* was examined with transmission electron microscopy (TEM); 2. pollen from all "species" of *Exochorda* was surveyed.

I undertook a broader sampling of *Exochorda*. The research was carried out in Beijing Agricultural College and Northeast Forestry University in China and Wageningen Agricultural University during 1994-1996. The purpose of the chapter is to present a summary of data, gathered largely through investigation with LM, SEM and TEM, that are relevant to an understanding of the diversity of pollen morphology within the genus, and to evaluate the systematic and evolutionary significance of ultrastructure variation in pollen of the genus.

4.2. Materials and methods

In eight provinces of China, in the main areas where *Exochorda* occurs, 22 populations and cultivated specimens were available for sampling of pollen. Details of their collection locations and vouchers are given in Table 4.1. Other materials were obtained from the collections of Wageningen Agricultural University (WAU). Voucher specimens of all accessions were deposited at the Herbarium Vadense (WAG), and voucher specimens of wild collections from China were also deposited at the Herbarium of Institute of Botany, Chinese Academy of Science, Beijing (PE). The pollen descriptions are based on all the light microscopy photographs, scanning electron microscopy photographs and transmission electron microscopy photographs.

Table 4.1. Voucher specimens of *Exochorda* collected in China

Name in previous classification	Pop.	Locality	Alt. (m)	Vouchers
E. racemosa (Lindl.) Rehder		Cult. in Nanjing Forestry University		Gao 0033
E. racemosa (Lindl.) Rehder	01	Qixiashan Mt., Nanjing, Jiangsu	150	Gao 0051
E. racemosa (Lindl.) Rehder	02	Chadaokou, Nanjing, Jiangsu	100	Gao 0052
E. racemosa (Lindl.) Rehder	03	Lingyan Shan Mt., Suzhou, Jiangsu	145	Gao 0056
E. racemosa (Lindl.) Rehder	03	Lingyan Shan Mt., Suzhou, Jiangsu	95	Gao 0061
E. racemosa (Lindl.) Rehder	04	Lingyan Shan Mt., Suzhou, Jiangsu	70	Gao 0062
E. racemosa (Lindl.) Rehder	05	Dengwei Shan Mt., Suzhou, Jiangsu	195	Gao 0063
E. racemosa (Lindl.) Rehder	06	Dengwei Shan Mt., Suzhou, Jiangsu	150	Gao 0064
E. racemosa (Lindl.) Rehder	07	Geling Mt,. Hangzhou, Zhejiang	150	Gao 0065

E. racemosa (Lindl.) Rehder	08	Zhongtianmen, Jigong Shan Mt., Henan	200	Gao 0075
E. racemosa (Lindl.) Rehder	09	Baoxiaofeng, Jigong Shan Mt.	710	Gao 0068
E. racemosa (Lindl.) Rehder	10	Longzikou, Jigong Shan Mt.	630	Gao 0069
E. racemosa (Lindl.) Rehder	11	Longzikou to Doushiya, Jigong Shan Mt.	580	Gao 0071
E. racemosa (Lindl.) Rehder	12	Doushiya, Jigong Shan Mt.	480	Gao 0073
E. racemosa (Lindl.) Rehder	13	Xianrenjing, Jigong Shan Mt., Henan	420	Gao 0074
E. giraldii Hesse	15	Heihuguan, Taibai Shan Mt., Shaanxi	1020	Gao 0077
E. giraldii Hesse	16	Jiaokou, Taibai Shan Mt., Shaanxi	1100	Gao 0079
E. giraldii Hesse	17	Hua Shan Mt., Huayin, Shaanxi	900	Gao 0080
E. giraldii Hesse	18	Shigao Shan Mt., Lingshi, Shanxi	1140	Gao 0081
E. serratifolia S. Moore	19	Wuling Shan Mt., Xinglong, Hebei	790	Gao 0083
E. serratifolia S. Moore	20	Fenghuang Shan Mt., Chaoyang, Liaoning	260	Gao 0085
E. serratifolia S. Moore	21	Haitang Shan Mt., Fuxin, Liaoning	400	Gao 0086
E. serratifolia S. Moore	22	Haitang Shan Mt., Fuxin, Liaoning	380	Gao 0087

Table 4.1 continued. Voucher specimens in Wageningen

Acc. No.	Name in previous classification	Locality	Coll. No.
--BG23207	*E. giraldii* Hesse	WAU	J.v. Veld. 1439
--BG22978	*E. giraldii* Hesse	WAU	J.v. Veld. 1437
85BGN3204	*E. x macrantha* (Lemoine) C.K. Schneid. 'The Bride'	WAU	J.v. Veld. 1438
85BGN0108	*E. x macrantha* (Lemoine) C.K. Schneid. 'The Bride'	WAU	J.v. Veld. 1441
87BGN0113	*E. x macrantha* (Lemoine) C.K. Schneid. 'The Bride'	WAU	J.v. Veld. 1435
--BG23206	*E. racemosa* (Lindl.) Rehder	WAU	J.v. Veld. 1443
84BG03409	*E. serratifolia* S. Moore	WAU	J.v. Veld. 1432
88BG16430	*E. serratifolia* S. Moore	WAU	J.v. Veld. 1433
--BG24250	*E. tianschanica* Gontsch.	WAU	J.v. Veld. 1444
85BG35601	*E. tianschanica* Gontsch.	WAU	J.v. Veld. 1436

Acc. No.: cult. in the Botanical Gardens, Wageningen Agricultural University.

4.2.1. LM

For light microscopy (LM), the materials were acetolysed according to Erdtman (1952) with minor modifications. To mount the pollen, a glycerine-water mixture (1:1) was added to the pollen suspension. After drying, the pollen grains were mounted in glycerine jelly, coverslip supports were added, then sealed with paraffin. The photography was performed with a ZEISS (Axiophot) microscope.

4.2.2. SEM

The materials used for scanning electron microscopic examination (SEM) were non-acetolysed. Pollen grains were taken directly from the anthers and then coated with gold for 4 min. The observations and photography were carried out with a KYKY 1000B scanning electron microscope.

4.2.3. TEM

For preparation for transmission electron microscopy (TEM), air-dried anthers were put into test tubes and pre-fixed with glutaraldehyde, then post-fixed in 2% osmium tetroxide, and buffered to pH 7.2 with phosphate buffer. After being dehydrated in a graded series of alcohol, they were embedded in Spurr's resin. The observations and photography were performed with a HITACHI H-600 electron microscope.

4.2.4. Measurements

With LM, the polar axis (P) and the corresponding equatorial diameter (E) were measured in equatorial view in 20 pollen grains per sample (10 pollen grains in a few samples). The distance between two colpus ends (A) and the corresponding equatorial diameter (E) were measured in polar view in 20 pollen grains per sample (10 pollen grains in a few samples). The values are given for P, E, P/E, A, E, and A/E, the average (between brackets), the minimum and the maximum.

With TEM the thickness of the exine and its individual layers were determined.

4.3. Results

Representative pollen grains are illustrated in Plate V, VI, size measurements and shape are summarized in Table 4.2. The shape is classified according to Erdtman (1964).

4.3.1. General morphology

Exochorda pollen grains are isopolar, three-colporate (Plate V), small or medium-sized, P = 20.9-30.5 (19.6-36.9) μm, E = 22.1-30.7 (17.9-35.7) μm; A = 5.2-9.5 (3.6-15.5). Grain shape is spheroidal (Plate V. 1-5) (only pollen of --BG23206 *E. racemosa*, cultivated in WAU is prolate) and P/E = 0.88-1.36 (0.81-1.73). The equatorial outline is obtusely triangular to subcircular, the triangular outlines usually have convex sides. The meridional outline is elliptic, obtusely rhombic or subcircular (Plate V. 4). The exine is composed of tectum, columellate layer and foot layer (Plate VI).

4.3.2. Apertures

Exochorda pollen is three-colporate (Plate V), The endo-apertures are usually lolongate. The colpi have acute ends. A/E = 0.20-0.32 (0.14-0.54).

Table 4.2. Variation of a number of pollen characters in *Exochorda*: equatorial view

Pop.	Coll.No.	P (μm)	E (μm)	P/E	Shape
	Gao 0033	22.0(23.1±0.8)24.5	22.0(23.6±0.8)24.5	0.92(0.98±0.05)1.06	spheroidal
01	Gao 0051	22.0(23.8±0.9)25.7	23.3(25.2±0.9)26.9	0.86(0.94±0.05)1.05	spheroidal
02	Gao 0052	20.8(22.8±1.2)25.7	22.0(24.1±1.0)25.7	0.86(0.95±0.04)1.00	spheroidal
03	Gao 0056	20.8(22.7±1.3)26.9	22.0(25.9±1.7)28.8	0.81(0.88±0.05)1.00	spheroidal
03	Gao 0061	20.8(23.3±1.0)24.5	22.0(24.8±1.2)26.9	0.86(0.94±0.04)1.03	spheroidal
04	Gao 0062	20.8(24.6±1.4)26.9	23.3(25.7±1.6)30.0	0.86(0.96±0.04)1.00	spheroidal
05	Gao 0063	22.0(23.7±1.3)26.9	22.0(23.9±0.9)25.0	0.90(0.99±0.05)1.10	spheroidal
06	Gao 0064	22.0(25.1±1.3)28.2	23.3(25.1±1.2)28.2	0.91(0.99±0.05)1.09	spheroidal
07	Gao 0065	22.0(23.4±1.0)25.1	20.8(23.7±1.1)25.7	0.86(0.99±0.07)1.18	spheroidal
08	Gao 0075	20.8(22.9±1.0)24.5	22.0(24.3±1.1)26.9	0.85(0.94±0.05)1.00	spheroidal
09	Gao 0068	22.0(23.8±1.1)25.7	23.3(24.4±1.1)26.9	0.90(0.97±0.04)1.08	spheroidal
10	Gao 0069	23.3(24.3±1.0)25.7	22.0(23.5±1.2)25.7	0.95(1.04±0.08)1.17	spheroidal
11	Gao 0071	23.3(23.6±0.5)24.5	24.5(25.2±1.0)26.9	0.86(0.94±0.03)0.98	spheroidal
12	Gao 0073	22.0(24.2±1.0)26.9	22.0(24.1±1.4)26.9	0.91(1.01±0.06)1.17	spheroidal
13	Gao 0074	19.6(23.0±1.3)24.5	22.0(23.4±1.1)25.7	0.82(0.98±0.08)1.11	spheroidal
15	Gao 0077	22.0(24.8±1.2)26.9	22.8(23.0±1.0)24.5	0.97(1.08±0.05)1.17	spheroidal
16	Gao 0079	22.0(23.5±1.0)24.5	22.0(24.6±1.2)25.7	0.90(0.96±0.04)1.06	spheroidal
17	Gao 0080	19.6(23.3±1.8)26.9	22.0(23.8±1.5)26.9	0.85(0.98±0.08)1.11	spheroidal
18	Gao 0081	19.6(21.3±1.5)24.5	19.6(22.1±1.0)24.5	0.89(0.96±0.07)1.12	spheroidal
19	Gao 0083	19.6(21.8±0.8)23.3	20.8(22.2±0.6)23.3	0.92(0.98±0.03)1.03	spheroidal
20	Gao 0085	19.6(20.9±0.8)22.0	19.6(22.0±1.3)23.3	0.89(0.95±0.05)1.06	spheroidal
21	Gao 0086	20.8(22.3±1.0)24.5	22.0(24.0±1.3)26.9	0.82(0.93±0.04)1.00	spheroidal
22	Gao 0087	22.0(23.7±0.9)25.7	22.0(23.3±1.0)25.7	0.95(1.02±0.03)1.06	spheroidal

Table 4.2 continued

-BG23207	22.6(25.7±2.1)31.0	21.4(24.9±1.9)29.8	0.87(1.03±0.09)1.22	spheroidal
-BG22978	25.0(29.6±3.4)36.9	17.9(27.1±3.1)35.7	0.88(1.13±0.22)1.60	spheroidal
85BGN3204	22.2(23.2±1.6)26.2	21.4(24.5±2.2)28.6	0.83(0.95±0.08)1.11	spheroidal
85BGN0108	26.2(29.3±1.8)33.3	26.2(28.7±1.3)31.0	0.88(1.02±0.08)1.18	spheroidal
87BGN0113	25.0(27.1±1.0)28.6	26.2(28.3±1.5)31.0	0.85(0.96±0.06)1.09	spheroidal
--BG23206	23.8(30.5±2.4)33.3	19.0(22.5±1.7)26.2	1.18(1.36±0.15)1.73	prolate
84BG03409	23.8(26.5±1.6)29.8	22.6(27.5±2.0)31.0	0.83(0.97±0.09)1.16	spheroidal
88BG16430	22.6(24.1±0.9)26.2	19.0(22.6±2.6)26.2	0.91(1.08±0.11)1.25	spheroidal
--BG24250	26.2(29.1±1.5)33.3	27.4(30.7±2.0)34.5	0.82(0.95±0.07)1.08	spheroidal
85BG35601	23.8(26.2±1.8)31.0	21.4(26.4±1.8)28.0	0.88(0.99±0.08)1.18	spheroidal

Table 4.3. Variation of a number of pollen characters in *Exochorda*: polar view

Pop.	Coll.No.	A (μm)	E (μm)	A/E
	Gao 0033	3.7(5.9±1.1)8.6	22.0(24.1±0.9)25.7	0.15(0.25±0.05)0.37
01	Gao 0051	4.9(6.3±1.0)8.6	24.5(26.5±1.0)28.2	0.18(0.24±0.04)0.32
02	Gao 0052	3.7(6.1±1.2)8.6	22.0(24.6±1.0)28.2	0.17(0.25±0.04)0.35
03	Gao 0056	4.9(6.3±1.6)9.8	23.3(25.4±1.4)27.6	0.18(0.25±0.06)0.40
03	Gao 0061	6.1(6.9±0.7)8.6	23.3(24.6±0.7)25.7	0.24(0.28±0.03)0.35
04	Gao 0062	4.9(6.6±1.5)11.0	24.5(26.9±1.3)28.2	0.14(0.20±0.06)0.35
05	Gao 0063	3.6(6.9±1.2)8.6	22.0(24.6±1.3)26.9	0.15(0.28±0.05)0.33
06	Gao 0064	3.7(6.2±1.3)9.8	24.5(26.5±1.1)28.2	0.14(0.24±0.05)0.36
07	Gao 0065	4.9(7.0±1.2)9.8	23.3(25.2±1.1)26.9	0.18(0.28±0.05)0.40
08	Gao 0075	3.7(6.6±1.3)8.6	22.6(24.7±1.3)28.2	0.16(0.27±0.05)0.35
09	Gao 0068	3.7(5.2±0.8)6.1	22.0(25.4±1.4)28.2	0.15(0.21±0.03)0.28
10	Gao 0069	3.7(6.7±1.5)9.8	23.3(25.8±1.3)26.9	0.14(0.26±0.06)0.36
11	Gao 0071	3.7(6.4±1.4)8.6	23.3(24.3±0.6)25.7	0.16(0.26±0.05)0.35
12	Gao 0073	4.9(6.8±1.1)8.6	22.0(25.1±1.5)28.2	0.21(0.27±0.04)0.35
13	Gao 0074	3.7(6.7±1.4)9.8	22.0(23.7±0.9)25.7	0.15(0.28±0.06)0.38
15	Gao 0077	4.9(6.4±1.2)9.8	22.0(24.3±1.3)25.7	0.19(0.27±0.05)0.37
16	Gao 0079	4.9(5.8±0.9)7.4	23.3(25.2±1.0)26.9	0.18(0.23±0.04)0.30
17	Gao 0080	4.9(6.6±1.0)8.6	22.6(24.5±1.0)25.7	0.20(0.27±0.04)0.35
18	Gao 0081	4.9(6.5±1.0)8.6	20.8(22.5±0.9)24.5	0.22(0.29±0.05)0.40
19	Gao 0083	4.9(5.9±0.9)7.4	20.8(22.4±0.7)23.3	0.21(0.26±0.04)0.33
20	Gao 0085	4.9(6.4±0.9)8.6	22.0(23.0±0.9)24.5	0.21(0.28±0.04)0.37
21	Gao 0086	4.9(6.4±0.9)7.4	22.0(24.3±1.4)28.2	0.20(0.26±0.04)0.32
22	Gao 0087	6.1(6.9±0.8)8.6	22.0(23.9±1.1)25.7	0.24(0.29±0.03)0.35

Table 4.3 continued

--BG23207	4.7(7.6±1.3)9.5	23.8(26.5±1.5)29.8	0.18(0.29±0.05)0.36
--BG22978	4.8(9.5±3.4)14.3	26.2(33.6±5.2)42.9	0.14(0.28±0.09)0.40
85BGN3204	6.0(7.1±1.5)10.7	21.4(25.2±2.0)29.7	0.20(0.29±0.07)0.47
85BGN0108	7.1(8.3±1.5)11.9	23.8(28.21.8±)32.1	0.22(0.29±0.05)0.37
87BGN0113	6.0(7.1±1.0)9.5	26.2(28.3±1.5)31.0	0.20(0.25±0.03)0.32
--BG23206	6.0(9.3±2.2)15.5	23.8(29.3±3.1)33.3	0.20(0.32±0.08)0.54
84BG03409	4.7(8.2±1.8)11.9	23.8(27.9 ±1.7)31.0	0.17(0.29±0.06)0.42
88BG16430	4.8(6.8±1.0)8.3	19.0(25.7±3.5)29.8	0.20(0.27±0.06)0.38
--BG24250	6.0(8.7±1.5)11.9	28.6(32.3±1.6)35.7	0.21(0.27±0.04)0.36
85BG35601	4.8(7.8±1.5)10.7	23.8(27.2±1.4)29.8	0.17(0.29±0.06)0.39

P: length of the polar axis.

E: equatorial diameter which is the length of the longest equatorial axis of a pollen grain.

P/E: the ratio of the length of the polar axis and the equatorial diameter of a pollen grain, which gives an indication of the shape of the grain in equatorial view (Erdtman, 1952).

A: apocolpium size, the distance between two colpus ends.

A/E: apocolpium size/equatorial diameter of polar view.

4.3.3. P/E value and shape of grain

P/E value in *Exochorda* relates to the shape of pollen grain. Figure 4.1 gives the P/E ranges of all samples and shows a continuous variation. The average P/E is 0.9976, it varies from 0.81 to 1.73. Grain shape is spheroidal (only --BG23206 is prolate).

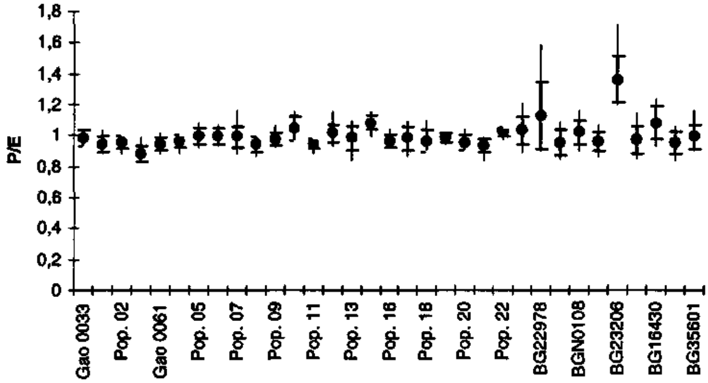

Figure 4.1. P/E ranges in *Exochorda* spp. pollen. Central symbol • : mean; ———: range (min., & max.); |——|: standard deviations.

4.3.4. A/E value and length of colpi

Figure 4.2 shows the A/E ranges in all investigated *Exochorda* samples. The average A/E is 0.27, it varies from 0.14 to 0.54. The result also shows continuous and only slight variation.

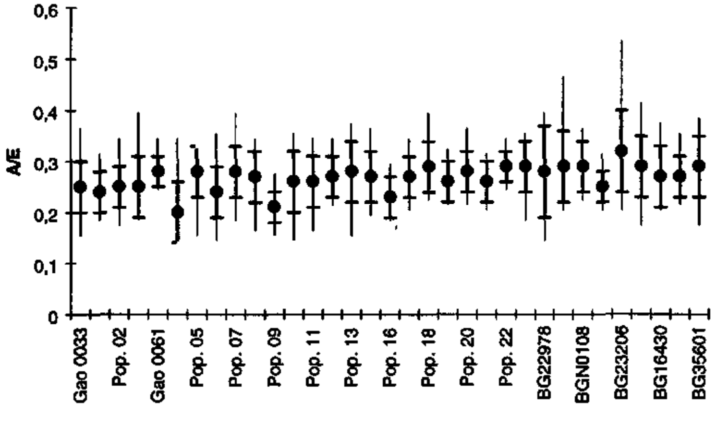

Figure 4.2. A/E ranges in *Exochorda* spp. pollen. Central symbol • : mean; ———: range (min., & max.); |——|: standard deviations.

4.3.5. Exine architecture

4.3.5.1. Stratification

Total exine thickness is 0.91-1.46 µm in the center of the mesocolpia. Usually it is quite uniform throughout the greater part of a mesocolpium; sometimes it decreases towards the colpi (Plate VI).

The tectum is 0.36-0.65 µm thick in the center of a mesocolpium. Sometimes it thins towards the colpi; or remains about uniform (Plate VI).

The columellate layer is 0.17-0.31 µm thick in the center of a mesocolpium. Usually it remains about uniform or it thins slightly towards the colpi, or thins out. The columellate layer is mostly absent along the colpi.

The foot layer is 0.32-0.51 µm thick in the central part of a mesocolpium. Sometimes it thickens near the colpi, foming a relatively thick layer under each colpus and the border of the adjacent mesocolpia. The foot layer thins towards the colpi (Plate VI. 2). There is thin intine under exine. Table 4.4 gives some character variation observed in TEM.

Table 4.4. Thickness (in µm)* variation of exine layers observed in TEM

Pop.	Coll.No.	Exine	Tectum	Columellate layer	Foot layer
01	Gao 0051	1.34	0.54	0.31	0.49
03	Gao 0056	0.93	0.40	0.17	0.36
09	Gao 0068	1.18	0.44	0.26	0.48
15	Gao 0077	1.18	0.51	0.25	0.42
18	Gao 0081	0.91	0.36	0.23	0.32
21	Gao 0086	1.46	0.65	0.30	0.51

* Measured in the centre of a mesocolpium, based on five measurements.

4.3.5.2. Ornamentation

Ornamentation in *Exochorda* pollen is rather uniform. One pollen type can be established on the basis of sculpturing and exine structure. It is striate (Plate V. 6, 7). Ornamentation is sometimes irregular in the mesocolpium. Smooth ornamentation was occasionally found in the apocolpium and shows little variation (Plate V. 6, 7).

4.4. Discussion and conclusions

In the genus *Exochorda*, pollen morphology and exine structure show little variation. In *Exochorda*, all samples share the same exine characters. Pollen grain shape of different species from different locations is spheroidal and rather uniform, with only one exception. This is concluded from a comparison of the P/E values of all gatherings (Table 4.2). With respect to P/E ratio, it is evident that all P/E values are between

0.88-1.36, pollen grain shape is spheroidal (a prolate shape was only found in sample -BG23206 cultivated in WAU). The pollen grains generally have convex sides. The photographs presented here are similar for light microscopy and scanning electron microscopy. When the variation of the shape is taken into account, it is clear that none of the available gatherings can be distinguished at the species level on the basis of the shape of their pollen grains. The range between the values of 20.94 µm and 25.10 µm is bridged by the values found in other field specimens which were investigated for their pollen grains. They cannot be interpreted as different taxa on the basis of dimensions of their pollen grains.

Table 4.5. Size of pollen grains (µm) in *Exochorda* from wild and cultivated plants

Species	Pw	Pc	Ccp%	Ew	Ec	Cce%
E. giraldii	23.2	27.7	+19.4	23.4	26.0	+11.1
E. racemosa	23.7	30.5	+28.7	24.5	22.5	-8.2
E. serratifolia	22.2	25.3	+14.0	22.9	25.1	+9.6

Pw: average length of the polar axis of wild material; Pc: idem of cultivated plants; Ccp: comparative difference of average length of the polar axis from the values calculated for cultivated plants to those of wild materials (%); Ew: average length of equatorial diameter of wild materials; Ec: idem of cultivated plants; Cce: comparative difference of average length of the equatorial diameter from the values calculated for cultivated plants to those of wild materials (%). For further explanation see the text.

In the present study, it was noticed that the size of pollen grains of cultivated plants often differs from that of plants collected in the wild. Table 4.5 shows the average dimensions of the polar axis (Pc) and the equatorial diameter (Ec) for some cultivated accessions. The comparative change (Cc) expresses the discrepancy between the average measurements of the wild and cultivated materials. For example, for the field collections of *E. racemosa*, the average length of the polar axis (Pw) is 23.7 µm. That of the cultivated specimens (Pc) is 30.5 µm. The grains of the cultivated specimens are on the average 6.8 µm longer than those of the field collections, an increase of 6.8/23.7=28.7%. The comparative increase of the polar axis ranges from +9.6% to 28.7% (Table 4.5). The length of the polar axis of cultivated specimens is in general longer than that of plants collected in field. The comparative change of the equatorial diameter is calculated similarly. But a decrease in Ec is found in *E. racemosa*. The deviation in the polar length as well as in equatorial diameter has an influence on the P/E ratio calculated for this collection. It may be assumed that growing conditions in nature differ in some ways from those in gardens. Löve & Löve (1975) wrote: "Cell size can also vary because of general differences between demes at the same level of polyploidy and it is affected by some environmental factors, so comparison ought to be made only between material grown under similar conditions". We postulate that differences between growth conditions in the forest and those conditions under cultivation (more advantageous) affect the size of cells, and this proved to be true of pollen grains in particular. In fact, the range between the values of these data is bridged by the values found in other field specimens which were investigated for their pollen grains. They cannot be interpreted as different taxa on the basis of dimensions of their pollen grains.

The ornamentation of *Exochorda* pollen has provoked debate. Wang Fushing (1995) considered pollen of *Exochorda* to be granulate-reticulate. My observations with SEM and TEM suggest that the surface sculpturing of *Exochorda* is striate (Plate V. 6, 7).

The data presented here support a close relationship between the previous taxa within *Exochorda*, as the morphology, ornamentation and stratification of these taxa are more or less identical. If we take into consideration these characters, all the samples are closely grouped due to similarities in these characters. These "species" have to be regarded as conspecific.

Rosaceae has a limited range of pollen morphology, in general pollen morphology of Rosaceae is quite similar (Wang Fushiung, 1995): i.e. isopolar, three-colporate, spheroidal or prolate, striate, reticulate or striate-reticulate. We know other genera of Rosaceae in which a comparable pollen diversity has been documented. Compared to other genera (Wang Fushiung, 1995), *Exochorda* pollen is similar to that of *Neillia*, *Sorbaria*, *Spiraea* and *Prunus*.

The study of pollen grains provides no evidence for a specific distinction within this genus, but it lends some support for a relationship with other genera in Rosaceae. Based on pollen morphology, *Exochorda* is similar to genera either in the subfamily Spiraeoideae or in Prunoideae.

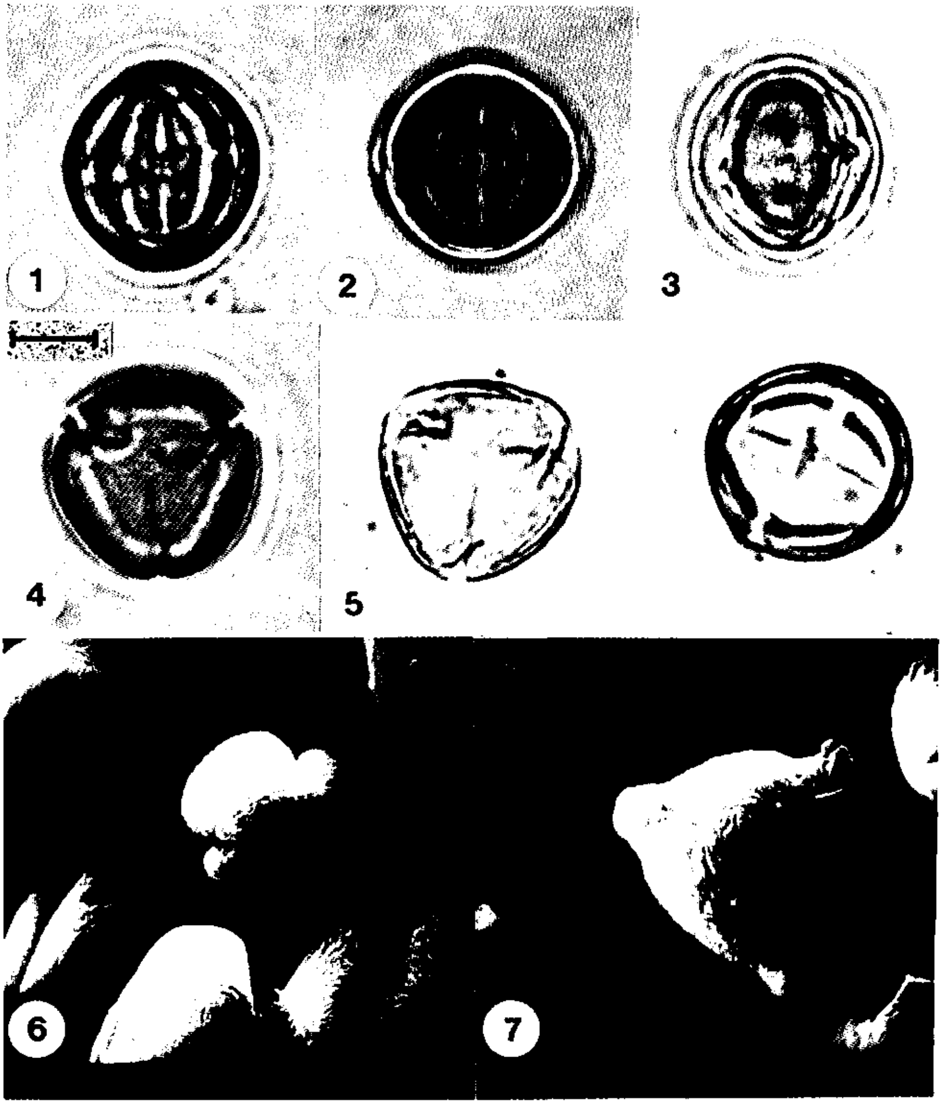

Plate V. LM photographs: 1-3. Equatorial view; 4. Polar view; 5. Polar & equatorial view. Sample 87BGN0113, bar = 12 µm. SEM photographs: 6. Polar & oblique view, sample Gao 0081 (Pop. 18), × 2000; 7. Polar view, sample Gao 0063 (Pop. 05), × 2000.

Plate VI. TEM photographs: 1. Cross section showing wall stratification, sample Gao 0081 (Pop. 18), × 4000; 2. Sample Gao 0086 (Pop. 21), × 6000. t = tectum, c = columellate layer, f = foot layer.

5. Cytotaxonomy

5.1. Introduction

The chromosomes play a special role as a source of comparative data in taxonomy, because these structures contain the genetic material which is responsible for maintaining reproductive barriers and the integrity of species and other taxa (Stuessy, 1990).

It has been realized that the more closely related species are, the more likely they are to have the same chromosome number; and the more distantly related, the more likely they are to have different numbers. This relative conservatism makes the chromosome number an important and much-used taxonomic character.

There are some reports about chromosome numbers of *Exochorda*: *E. giraldii* Hesse, 2n = 16 (Sax, 1931a); *E. korolkowii* Lavallée, 2n = 16 (Rusanov, 1977).

The aim of the present work is to obtain more information on chromosome numbers of *Exochorda* spp. for their classification.

5.2. Materials and methods

The material was collected in China and the Botanical Gardens of Wageningen Agricultural University, the Netherlands (Table 5.1). Voucher specimens of all accessions were deposited at the Herbarium Vadense (WAG) and voucher specimens of wild collections were also deposited at the Herbarium of the Institute of Botany, Chinese Academy of Science, Beijing (PE).

Table 5.1. Seed collections in China and WAU

Names	Locality*	Pop.	Vouchers
E. giraldii	Heihuguan, Taibai Shan Mt., Shaanxi	15	Gao 0111
E. korolkowii	Cult. in WAU		BG22613
E. x macrantha 'The Bride'	Cult. in WAU		87BGN0113
E. racemosa	Lingyan Shan Mt., Suzhou, Jiangsu	03	Gao 0091
E. racemosa	Dengwei Shan Mt., Suzhou, Jiangsu	05	Gao 0103
E. racemosa	Geling Mt., Hangzhou, Zhejiang	07	Gao 0090
E. racemosa	Baoxiaofeng, Jigong Shan Mt., Henan	09	Gao 0107
E. racemosa	Longzikou to Doushiya, Jigong Shan Mt., Henan	11	Gao 0108
E. serratifolia	Wuling Shan Mt., Liaoning	19	Gao 0089
E. serratifolia	Fenghuang Shan Mt., Liaoning	20	Gao 0117
E. serratifolia	Haitang Shan Mt., Liaoning	21	Gao 0120

*Further information was given in Chapter 1.

Seeds were soaked in tap water at room temperature for 24 h and then put into petri dishes on wet filter paper at room temperature to germinate. Root tips were obtained from the germinating seeds. Three methods of pretreatment were applied for chromosome shortening. 1. Pretreatment in an aqueous solution of 0.1% colchicine at room temperature for 3 h; 2. Pretreatment in an aqueous solution of 2 mM 8-hydroxy quinoline (0.029g/100ml) at room temperature for 2.5 h; 3. Pretreatment in an ice and water mixture at 4° C for 24 h. After pretreatment, the root tips were fixed in Carnoy I fixative (ethanol-acetic acid 3:1) for 20 h. To make a preparation, root tips were briefly rinsed in Milli-Q water, hydrolyzed in 1 N HCl at 60° C for 10 min, and rinsed again. Subsequently, the root tips were squashed in 45% acetic acid on a glass glide and frozen at -20° C overnight. The cover slip was removed and the slide was rinsed briefly in Carnoy I and 96% ethanol respectively. The slide was air-dried, stained in 1% Giemsa for 3 min, rinsed briefly in Milli-Q water, air-dried and mounted in DPX .

Metaphases with well-spread chromosomes were selected and photographed with a ZEISS Axiophot (Kodak film).

5.3. Results and discussion

It was difficult to obtain large numbers of metaphase plates with either of the three methods of pretreatment, but the second method was better than the others. All the metaphases with well-spread chromosomes were from the second method. Two different chromosome numbers were observed, i.e. 2n = 16, 2n = 18. The chromosome numbers for different collections are shown in Table 5.2.

There is little difference in chromosome character between different accessions. The chromosomes are small, 1-2 μm; there is little difference between different pairs, the structure is basically homotype; symmetry is high; no satellite chromosomes were observed.

It has been realized from the early years of this century that, in general, the number of chromosomes in each cell (the chromosome number) of all the individuals of a single species is constant (Stace, 1989). But some literature (Fedorov, 1974) also reported different chromosome numbers in one species. Within species the variation in number tends to be less, but one can cite *Chaenactis douglasii* (Compositae: Mooring, 1965) as an extreme example of variation (2n = 12, 13, 14, 15, 18, 24, 25, 26, 27, 28, 36, and ca. 38) (Stuessy, 1990). As shown in Table 5.2, we often found two chromosome numbers in one plant of *Exochorda* or in the same root tip preparation.. The reasons could be: 1. chromosomes can be broken when squashed; 2. presence of satellite chromosomes; 3. there are two chromosome numbers in *Exochorda* for different cells, i.e. 2n = 16, and 2n = 18. It should be pointed out that more research is needed to gather conclusive evidence.

Table 5.2. Chromosome numbers for different accessions of *Exochorda*

Names in previous classification	Pop.	Chromosome No.	Reported by
E. giraldii		2n = 16	Sax, 1931a; Darlington, 1955
E. giraldii	15	2n = 18	Gao, 1998 Fig. 5.1
E. korolkowii		2n = 16	BG22613 Fig. 5.2
E. korolkowii		2n = 16	Rusanov, 1977
E. x macrantha 'The Bride'		2n = 16; 2n = 18	Gao, 1998 Fig. 5.3
E. racemosa	03	2n = 16	Gao, 1998 Fig. 5.4
E. racemosa	05	2n = 16	Gao, 1998
E. racemosa	07	2n = 18	Gao, 1998
E. racemosa	09	2n = 16	Gao, 1998
E. racemosa	11	2n = 18	Gao, 1998
E. serratifolia	19	2n = 16; 2n = 18	Gao, 1998
E. serratifolia	20	2n = 16; 2n = 18	Gao, 1998
E. serratifolia	21	2n = 16; 2n = 18	Gao, 1998
E. tianschanica		2n = 16	cf. Fedorov, 1974
E. tianschanica		2n = 18	Gao, 1998

The analysis of DNA content of nuclei isolated from leaf tissue showed that all the *Exochorda* samples have a relative low DNA content compared with a known plant *Lycopersicon esculentum* L. 'Tiny Tim'. In all *Exochorda* plants analyzed, relative DNA content rang from 48-52. This result indicated that genotypes in the *Exochorda* complex have a low DNA content and variation among different "species" is small.

We found it is impossible to use chromosome data to distinguish previously recognized taxa in the complex. But it can provide some support for the position of the genus in Rosaceae.

Based on cytological evidence of *Exochorda* (x = 8), Goldblatt (1976) suggested that "its transfer to the Prunoideae appears warranted", this treatment "may be the most satisfactory way to reflect the natural relationships of the genus".

According to my data of two chromosome numbers (2n = 16, 2n = 18), I did not see much evidence for this taxonomic opinion. In my opinion, *Exochorda* occupies a singular place between Spiraeoideae (x = 8) and Prunoideae (x = 9), and the genus constitutes a link between both subfamilies with these two numbers.

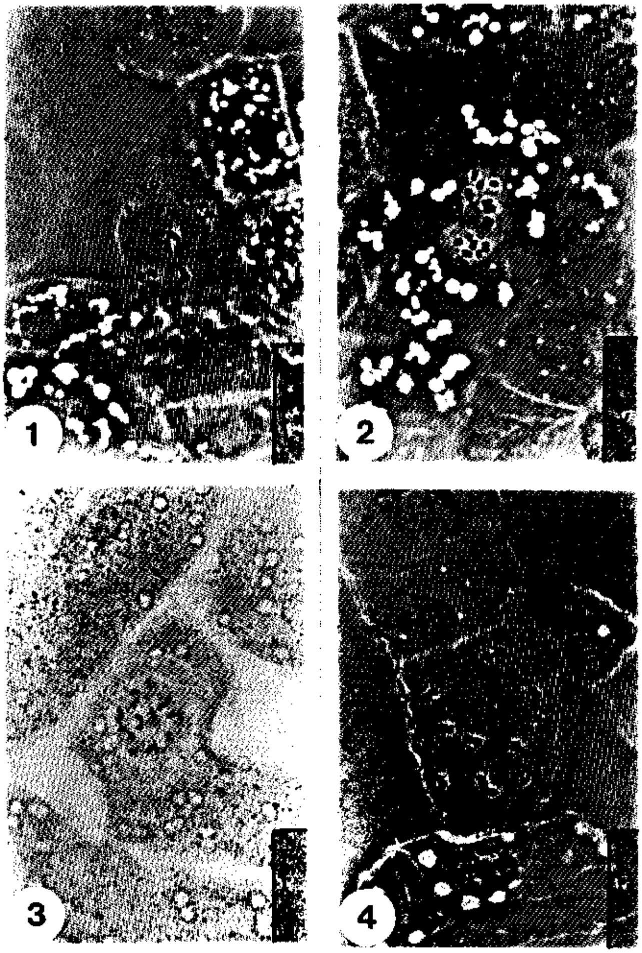

Figure 5.1-4. Metaphases of *E. giraldii* (1), *E. korolkowii* (2), *E. x macrantha* 'The Bride' (3), *E. racemosa* (4), bar = 4.9 μm.

6. Embryology of *Exochorda*

6.1. Introduction

Various studies on comparative morphology of the carpel in Rosaceae have been reported (Sterling, 1964, 1965, 1969; Rohrer et al., 1994). There has long been a need more detailed investigations of embryology in the genus *Exochorda*, as previous work (Johnston, 1961; Van Heel, 1976) concerned studies on the microsporangium of this genus. In this chapter, the microsporangium and microsporogenesis, megosporangium and megagametogenesis of *Exochorda* were studied. The research was carried out in Beijing Agricultural College, Beijing and Wageningen Agricultural University (WAU), the Netherlands during 1994-1996. The aim of the research was to contribute knowledge for the systematic place of *Exochorda* in an evolutionary sense.

6.2. Materials and methods

Inflorescences with buds, and flowers of *Exochorda racemosa* (Lindl.) Rehder were collected from the nursery, Chinese Academy of Sciences, Beijing from February to May 1994-1996, and were fixed in FAA.

Preparations of microtome sections for observations were made by standard paraffin methods. Serial sections 8-10 µm thick were stained with safranin and fast green. The photography was performed with a ZEISS (Axiophot) microscope.

6.3. Results

6.3.1. Pistil

The pistil of *Exochorda* is composed of 5 carpels (occasionally by 4 or 6 carpels represent aberrant forms) and consists of ovary, style and stigma. The ovary is superior. Stigmas and styles are free. The pistil is c. 3 mm long when flowering and slightly shorter than the stamens. The ovary of fused carpels is partitioned into 5 locules (Fig. 6.1) containing 2 ovules (or 1). The placentation is apical, pendulous. The ovules are anatropous, bitegminous and crassinucellate.

The style has a central style path (transmitting issue) and is approximately cylindrical. The carpel terminates in a somewhat grooved stigma in order to expand the receptive surface (Figs. 6.1, 2). At flowering, the carpels are united at the level of the lowermost ovular insertion, but longitudinal and transverse sections of the carpel show that the sutures are incomplete among carpels, only united in the axil (Fig. 6.3), thus resulting the carpels are more or less free, i.e. the tegument may open at lower level, when mature, capsules burst open along these seams.

The wall of the ovary consists of an outer epidermis and 1 or 2 inner epidermis layers, parenchyma and dosal and ventral traces (Fig. 6.3). At flowering the epidermis is a single layer of cells without any appendages which are arranged closely. The 1-2 inner epidermis layers stained red are larger and are loosely arranged.

Each carpel is supplied with some traces. The centrals (ventral veins) run along the axil of the carpel, while the laterals (dorsal veins) run along the abaxial side of the carpel. Two of the central veins can reach the surface of the stigma. The dorsal veins and the ventral veins are connected by numerous branching veinlets and the terminate in short tracheids.

Some special cells in the center of the style are transmitting tissue (Figs. 6.2, 4). From the longitudinal section, it is observed that these cells are long and narrow with copious cytoplasm. Transverse sections of the stigma show that the transmitting tissue appears at the center of the stigma as a group of small cells with large nuclei and concentrated cytoplasms without vacuole. Pollen tubes growing in the transmitting tissue could not be observed.

6.3.2. Microsporangium and microsporogenesis

Microsporogenesis is the formation of microspores within the microsporangia, or pollen sacs, of the anther.

Flowers, including about 15-30 stamens, originate in the bracts of a raceme. Anthers have four pollen sacs (Fig. 6.6), which is a feature found in most angiosperms. The anther wall is composed of five cell layers, i.e., epidermis, endothecium, two middle layers and the tapetum (Fig. 6.6). The epidermis is a layer of narrow and tangentially elongated cells. The endothecium has radially elongated cells that are fibriform at the tetrad stage. The middle layer is two cells thick and the innermost layer is the tapetum. The wall formation, prior to maturity, conforms to the Basic type as defined by Davis (1966). The four microspore protoplasts may be walled off simultaneously after the second meiotic division. Meiosis of microspore mother cells is of the Simultaneous type. At the tetrad stage, tapetal cells have 2-4 nuclei and begin to degenerate but still remain in their original position (Fig. 6.8). Therefore, the tapetum belongs to the Glandular type. When mature, the tapetal cells and the middle layers degenerate and the endothecium become enlarged, developing a fibrous thickening. The mature pollen sac wall is composed of only one fibrous layer which is covered by epidermis. All the microspores in the tetrads are tetrahedral (Figs. 6.8, 9).

The meiosis of microspore mother cells is not synchronous in the same locule in one anther, there is a 1-2 period difference.

Mature pollen grain is isopolar, three-colporate, small or medium size, $P = 24.54$ (19.54-36.90) μm, $E = 24.75$ (17.90-35.70) μm. Grain shape is spheroidal. The ornamentation is striate (see Chapter 4: Pollen morphology).

6.3.3. Megasporogenesis and megagametogenesis

Megasporogenesis is the process of megaspore formation within the nucellus tissue (megasporangium) of the ovary. Megagametogenesis is the development of the megaspore into the megagametophyte.

The archesporial cells originate the cells which is divided periclinally (Fig. 6.11). The differentiation of primary parietal cell, sporogenous cell and megaspore mother cell could not be observed.

From Fig. 6.12, it is inferred that three megaspores from the micropylar end degenerate, and the megaspore at the chalazal end becomes functional.

After the first mitosis of the functional megaspore, the central vacuole continues to enlarge, one of the two nuclei migrates to the micropylar end and the other to the chalazal end. Therefore, 2-nucleate embryo sac contains a large central vacuole (Fig. 6.13). The mature embryo sac is of the Polygonum type, and has one egg cell and two synergids at the micropylar end, three antipodal cells at the chalazal end, and two polar nuclei in the centre (Figs. 6.14-16). The last two soon fuse to form secondary nucleus. The antipodal cells gradually disappear as the embryo sac matures

A normally developed proembryo, and embryo have not been observed in the hundreds of slides that were prepared, probably due to abortion of most fertilized egg cells or non-fertilization of egg cells. It could be inferred that this embryological pattern, which probably reduces the reproductive capacity of *Exochorda*, could be considered as another major biological factor causing low fruit set (see Chapter 7: Pollination of *Exochorda*).

6.4. Discussion

The development of the carpels and the knowledge of this basic structure in angiosperms are important for understanding the systematics and the evolution of angiosperm families and genera, especially of the primitive taxa (Chapman, 1936; Bailey & Nast, 1943; Bailey & Swamy, 1951; Canright, 1960; Van Heel, 1981).

The origin and homology of the carpel has been discussed for more than a century. The theory that carpels are leafy structures and should preferably be compared with foliage leaves is most widely accepted. Based on this basic concept two modified theories are apparent: Bailey et al. (1951) considered that carpels are conduplicate leaflets fused at the margins; Endress (1980) and Van Heel (1981) believed that carpels are morphologically peltate leaflets which are ascidiate at the base and plicate above.

According to the conduplicate theory, in the primitive type of angiospermous carpel, the ovuliferous organ is regarded as essentially being a stalked, folded (conduplicate) megasporophyll. Conduplicate carpels (illustrated by Bailey & Swamy, 1951) are usually supplied with three vascular strands, the dorsal vein running through the abaxial carpel wall, and the two ventral veins beneath the adjacent margins on the adaxial side. The ovules are anatropous, and supplied by vascular strands derived from either the ventral or the dorsal bundles.

It is evident that the carpel characters of *Exochorda* resemble those of the primitive carpel postulated above. These included: incomplete carpel closure, anatropous ovules. *Exochorda* has its ovary partly united, whereas the subfamily Spiraeoideae generally has separate carpels. This character again stresses the singular place of *Exochorda* within Rosaceae.

About low fruit set, the possibilities could be: the pollen grain does not germinate on the stigma or developing pollen tube interacts with the style in such a way that the male nuclei do not reach the egg cell. On the other hand, a limited source of carbohydrates may cause low fruit development even after fertilization of egg cells.

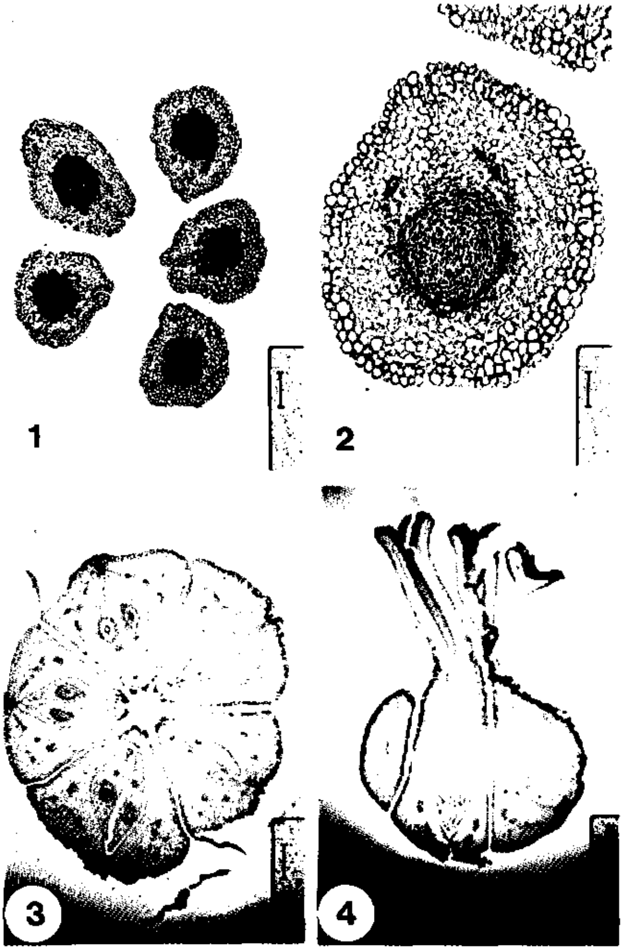

Figure 6. 1-4: Transverse section of the styles, showing five free stigmas, bar = 63 µm; 2. Transverse section of one style, showing style path, bar = 185 µm; 3. Transverse section of lower ovary, showing five partly united carpels and central traces, bar = 310 µm; 4. Longitudinal section of pistil, showing style path, bar = 185 µm.

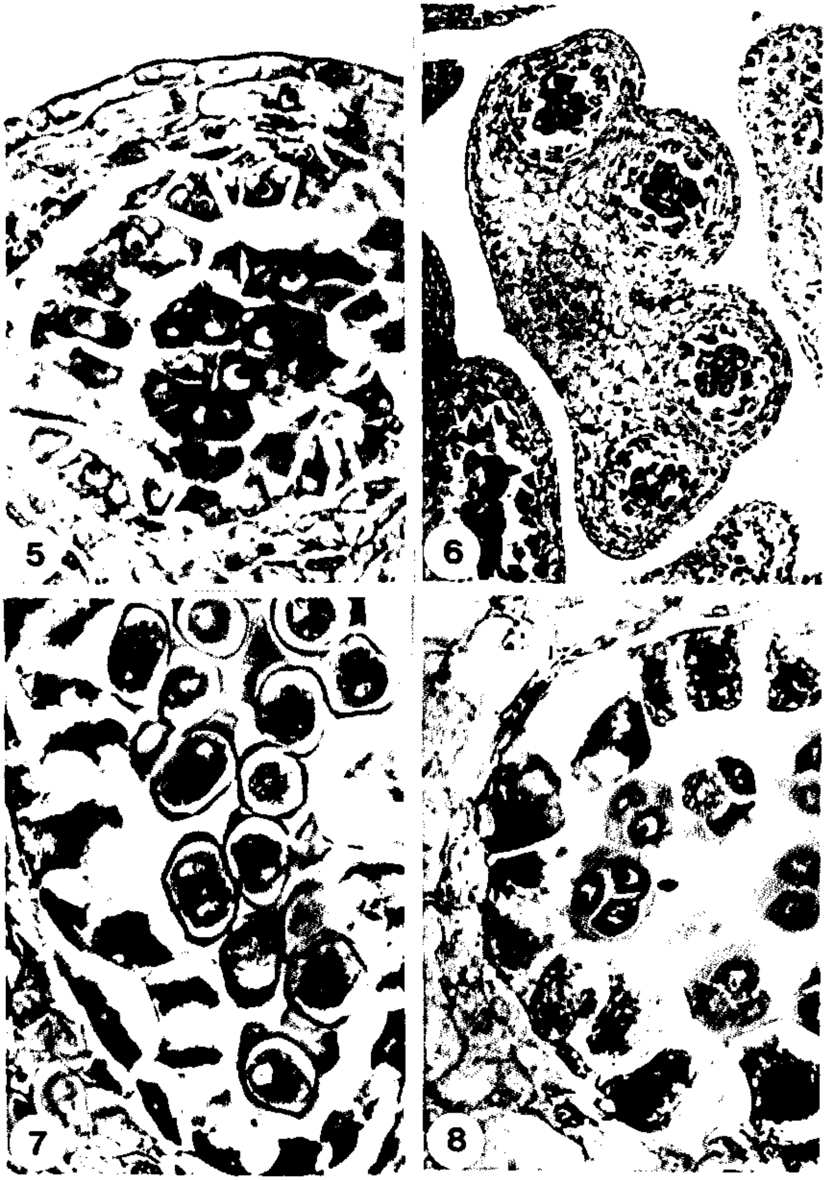

Figure 6. 5-8: 5. One locule, showing the secondary sporogenous cells surround by the fully differentiated anther wall, × 600; 7. Transverse section of the anther, showing four pollen locules, × 40; 7. Microspore dynads, × 600; 8. The tetrads and tapetum, × 600.

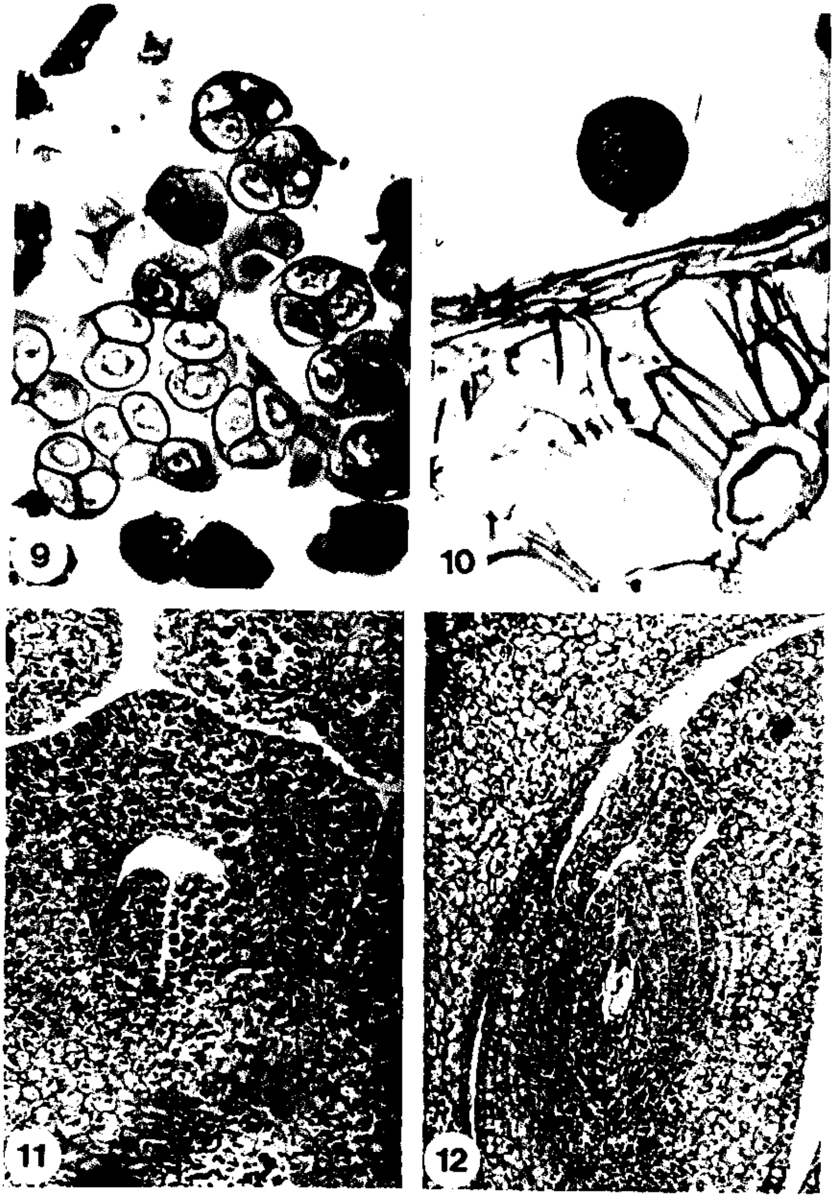

Figure 6. 9-12. 9.Tetrahedral tetrads, × 600; 10. Transverse section of the anther, showing one pollen grain, × 600; 11. Longitudinal section of a young flower, showing the emergence of ovary, × 400; 12. The three megaspores from the micropylar end degenerate, and the megaspore at the chalazal end becomes functional, × 400.

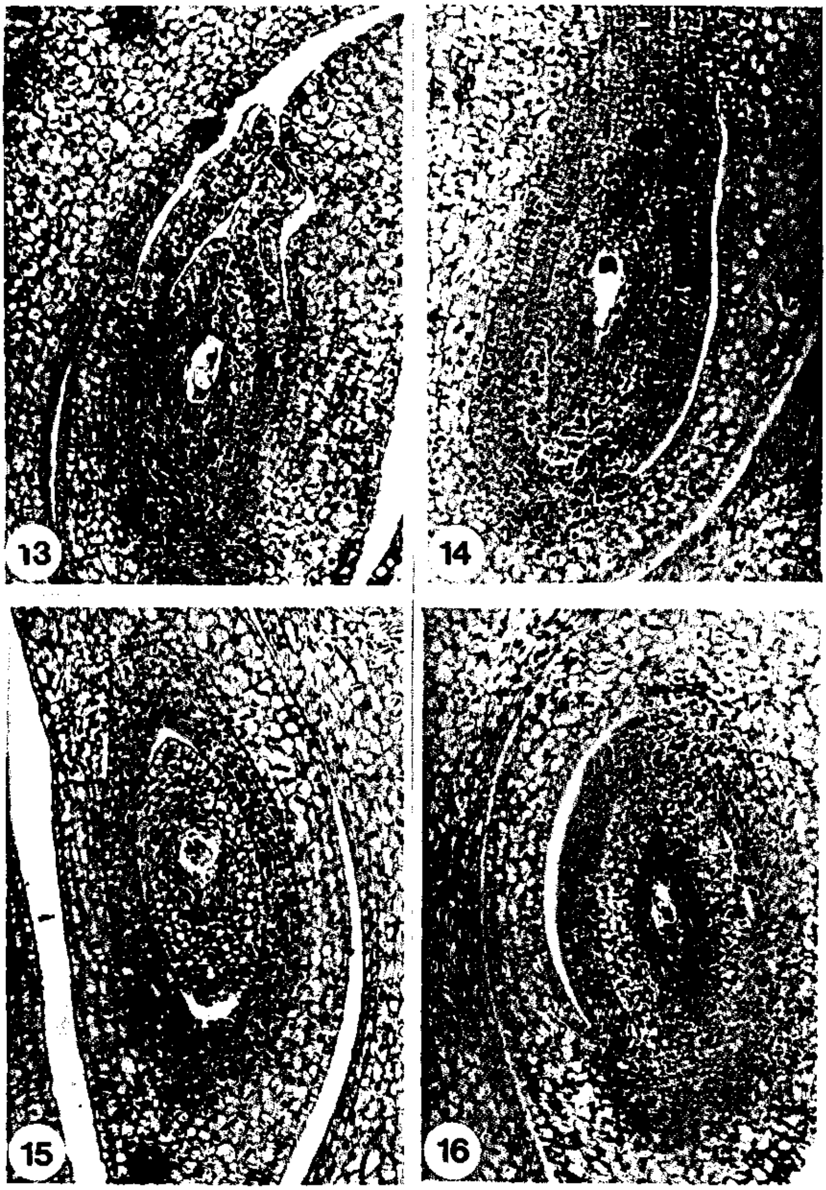

Figure 6. 13-16. 13. A bi-nucleate embryo sac, × 400; 14. Longitudinal section of an ovule, showing two synergids, × 400; 15. Longitudinal section of an ovule, showing two synergids, × 400; 16. Longitudinal section of an ovule, showing central cell and antipodal cells, × 400.

7. Pollination of *Exochorda*

7.1. Introduction

Exochorda is distributed in East and Central Asia, particularly in China and the Central Asian republics of Kirghizstan, Tadzhikistan, Turkestan and Uzbekistan from 29°10' N to 42°00' N, and from 105°40' E to 128°00' E. The conditions are continental climate, depending on the prevailing environmental conditions, the populations start to flower from late March in the south to the middle of May in more northern locations.

Pollination biology is growing because of its contribution to population genetics, ecology, conservation biology and systematic and evolutionary biology. The first discoveries of cross-pollination are said to be due to A. Dobbs (1750) and H. Müller (1751) who also discovered the role played by insects in pollination (Fægri & van der Pijl, 1979). However, two other botanists, Koelreuter & Sprengel, are generally accepted as the founders of pollination ecology (Fægri & van der Pijl 1979). The first botanist to carry out hybridization on a large scale for scientific purpose was J.G. Koelreuter. Observations of pollination were first made at the end of the 18th century (Sprengel, 1793). He discovered the mutual adaptation of flowers and their pollinators. Observation of pollination followed by Robertson (1892), Knuth (1898-1905) and others. The study of experimental pollination biology has been conducted till the eighties of the 20th century (Harley, 1971; Fægri & van der Pijl, 1979; Keller & Armbruster, 1989). Nevertheless, there is still a shortage of pollination data in Rosaceae and for *Exochorda* no published data could be found. The aim of this study was to contribute to the knowledge on reproduction of *Exochorda*. My interest in the pollination biology of *Exochorda* also regarded a frequently encountered phenomenon: why does *Exochorda* produce more flowers than fruits?

The interaction between plant and animal requires that the ecological conditions are suitable to allow this interaction. Such interaction is expressed in the relation of the flower to its visitors. The combination of flower and its visitors leads to a pollination syndrome, the specific way of pollination.

Plants depend on insect (and abiotic factors) to transport pollen for the reproductive process, and insects collect pollen and nectar offered by the plant for nutrients. In many cases, the flower is also a place for an insect to hide, warm up or oviposit. Close ties exist between plant and insect.

The proportion of flowers that produce fruit, the fruit set level, is highly relevant to a plant's reproductive success (Guitian, 1993). Low fruit set levels have been documented in numerous hermaphroditic plants (Stephenson, 1981; Sutherland & Delph, 1984; Sutherland, 1986a; Guitian, 1993). In many species, it is found that some flowers do not produce fruit.

have a life span of only a few weeks, which restricts them to specialize on very few plant species (Linsley, 1958). In Beijing, solitary bees and social working bees constitute the majority of Rosaceae pollinators.

The pollination of *Exochorda* was investigated during 1995-1997 with respect to: 1: low fruit set of *Exochorda*. 2: the pollination-based relationships between *Exochorda* and their pollinators in the community context of a biotope; 3: species of pollinators; 4: behaviour of pollinators.

7.2. Materials and methods

7.2.1. Site

The study was conducted in the Xiang Shan Mt., 116°28' E, 39°48' N, situated about 18 km west of the centre of Beijing, in the area of the Botanical Garden, Institute of Botany, Chinese Academy of Sciences at an altitude of 76 m. Secondary forest and cultivated trees are the dominant ecosystem types. In the Botanical Gardens of Wageningen Agricultural University (WAU) in the Netherlands, there are extensive collections of *Exochorda* as well, offering the opportunity to perform pollination research there. For the wild populations, the natural conditions are primary forest and deforested areas in the temperate zone. For some climatic details see Appendix III. As can be seen, in nature temperature ranges have a large amplitude than the Netherlands climate, and the rainfall can be both higher and lower.

7.2.2. Plant species and floral biology

Three "species" are cultivated in the study area of Beijing. These are: *E. giraldii* Hesse, *E. racemosa* (Lindl.) Rehder and *E. serratifolia* S. Moore. In the study area, the flowering period extends from April to May, and fruits mature in September. The features recorded were corolla colour, inflorescence length, corolla size, flower life span, pollinators and fruit set. The samples consisted of 20 flowers that were collected at random.

Colour: Colour identification was made on site by two persons, independently presented with the 20 flower samples. All three "species" have a pure white corolla.

Inflorescence length: Based on 20 inflorescences at random, the length was always measured from the topmost leaf or vegetative bud under the inflorescence. They varied from 57.7 mm to 88.5 mm. The distance between two flowers was also considered (Table 7.1).

Flower size: The diameter of the plane projection of the largest surface was considered for flower size determination (Dafni, 1991). The size measured is presented for 20 flower samples. The diameter ranges from 37.3 mm to 42.9 mm (Table 7.1).

Flower life span: The flower life span includes two aspects: one is the life span of a single flower; the other is the life span of an inflorescence. During flowering time, 20 flowers and 20 inflorescences were observed on a daily basis from their opening to their wilting. The mean values were reported.

Table 7.1. Mean values of floral parameters of different "species" in Beijing and Wageningen

Names in previous classification	Coll. No.[a]	1	2	3	4
E. giraldii [b]		58	6	11	43(38-51)
E. racemosa [b]		72	8	10	37(31-43)
E. racemosa [c]		89	10	9	41(33-48)
E. serratifolia [b]		67	9	10	43(36-53)
E. giraldii		79	7	11	37(33-40)
E. giraldii		92	9	10	38(34-40)
E. korolkowii	--BG24250	87	9	10	35(27-43)
E. x macrantha 'The Bride'	87BGN0113	75	8	9	38(30-45)
E. serratifolia	--BG03409	80	6	15	39(32-45)
E. tianshanica	85BG35601	86	8	11	34(28-40)

[a]: accession number of collection in the Botanical Gardens of Wageningen Agricultural University.

[b]: in the Botanical Garden of Chinese Academy of Sciences, Beijing.

[c]: plants in population 01, Qixia Shan Mt., Nanjing, Jiangsu province.

1: average of inflorescence length (mm).

2: number of flowers in one inflorescence.

3: average of distance between two flowers (mm).

4: average and range of flower size (mm).

7.2.3. Pollinators

During the flowering period, pollinators which made contact with the flower's reproductive organs were recorded. This is considered to result in pollination of a visited flower (Fægri & van der Pijl, 1979). During the flowering period, observations were made every hour from sunrise to sunset for 3 days in 1996 (in Beijing), each lasting 15 min. The insect identification was made by specialists up to species level (some restricted to genus or family level). Voucher specimens of insects are kept in Beijing Agricultural College. The list of the insects is given in Table 7.3.

7.2.4. Fruit set

During 1995-1997, some branches of adult individuals of *Exochorda* were marked as a control along a transect. The following treatments were applied:

1. **Treatment 1: insect exclusion:** branches (with unopened flowers) were bagged with gauze bags to prevent pollinator access; The branches closest to the bagged branches were marked and used as control.
2. **Treatment 2: self-pollination** (anthers of marked flowers were removed before pollen dehiscence): using a fine paint brush, pollen from the same plant was applied to these flowers. The flowers were bagged.
3. **Treatment 3: cross-pollination** (i.e. xenogamous) (anthers of marked flowers were removed): using a fine paint brush, pollen from other *Exochorda* shrubs of different "species" was applied to these flowers. The flowers were also bagged. These treatments were repeated two times during the flowering period to ensure that the treatment coincided with stigma receptivity.

Bags were removed after all flowers or flower parts (except the pistil) had fallen off in Wageningen Agricultural University, but not removed in Beijing.

7.3. Results

7.3.1. Plant-animal interaction

Plants use odour, shape, colour, pollen and nectar of flowers to attract insects.

Exochorda has racemes which bear young flowers on the top of the peduncle. There are slight differences in absolute size of structures (see Table 7.1), but the relative proportions and sequence of development of all the cultivated accessions are the same. At the basal part, open flowers offer a place to land. The inflorescence is visited in a vertical direction to the top, the inverse direction is also possible. The position of the inflorescence is erect and oblique, to enable passage over the single flower. The plants in the study areas share a flowering time from mid-April to May. The most extended flowering period lasts 10 days. The life span of a single flower is 2 days; and the life span of one inflorescence is about 5 days; the total flowering period of one plant can last 20-25 days. Individual flowers tend to open for the first time in the morning or afternoon. The lowest flower of a raceme opens first, the others will follow gradually. This is in accordance with the normal rule in racemes, namely, the order of flowering in a racemose inflorescence is typically in upward (acropetal) sequence. The successive opening in an inflorescence is also of a great biological advantage against the momentary opening of a single flower (Takhtajan, 1991). By a sequential maturation of the flower, the plant can offer an extended period for visits by pollinators. Each pollinator can visit more flowers assembled in an inflorescence than solitary flowers per unit of time (Takhtajan, 1991).

The petals are round at the apex or somewhat emarginate, at the base there is a short or long claw, the limb is elliptic. The petals are free and do not overlap within one flower, but they overlap other flowers. In general, they attract pollinators by long-distance advertising of the flowers. In the flower a green nectariferous disk attracts many insects, and nectar is produced in quantities large enough to be visible and to smell the odour. Flowers of *Exochorda* produce a moderately strong, sweet odour. The odour is strongest during the day in flowers exposed to full sun, and weakens when the flowers are withering. Around the disk, five groups of stamens are inserted opposite to the petals, each bundle consisting of 3-6 stamens, so the number of stamens varies from 15-30. From the beginning of flowering, in every group of stamens, the outer two turn outwards and the central stamens remain in a reflected position, forming 30°-40° angle. At first view, there are two rings of stamens, but in fact all stamens are inserted at the edge of the disk.

When the petals start to unfold, the outer stamens of each group open by longitudinal slits and shed pollen, and the pollen adheres to the outer surface of the anther until removed by a pollinator. While the central stamens remain closed and cover the stigmas, so the stigmas are not exposed at the beginning of anthesis. Thus self-pollination is partly precluded if outer anthers dehisce and shed their pollen at a time when the stigma is not receptive. At this time, the pistil is approximately 0.5 mm long, with five short styles which form a small, viscid knob at the tip of each style. With the development of flowers, filaments become erect, all stamens shed pollen, five stigmas are nearby, thus it would be easy for stigmas to pick up much pollen resulting in self-pollination. When the petals open completely, the anthers wither, and then the stigmas expand, nectar production ceases and pollination will be finished.

With the saucer-shaped flower, *Exochorda* offers an easy landing place for insects. When large insects such as the bumble bee *Bombus speciosus* Smith. and the butterfly *Pieris rapae* L. pay a visit to the reproductive organs, they land on a petal, and suck nectar and pollen with their long mouth parts. Small insects such as the bee *Apis cerana* Fabr. and hover flies *Syrphus* spp. land on anthers and stigmas and suck pollen and collect nectar from the disk. By visiting the flowers, insects are instrumental in pollination.

It is noticed from the observations that the first and the last formed flowers differ in quality of pollen and pistils. In general, in a single flower either the pistils or the stamens are well-developed, rendering it functionally dioecious. In some flowers (mainly the upper flowers) pistils are not well-developed, hence not functional, thus acting as male flowers. Table 7.2 shows the ratio of flowers with degenerate pistils. Another phenomenon associated with *Exochorda* is that when the apical flower opens, the 2 to 3 subtending flowers will wilt. This phenomenon leads to a lower fruit set and also affects the number of seeds per plant.

Table 7.2. Percentage of degenerate pistils

Species in previous classification	Coll. No. [a]	Degenerate pistils (%)
E. giraldii [b]		36
E. racemosa [b]		30
E. serratifolia [b]		46
E. giraldii	--BG23207	75
E. giraldii	--BG23209	41
E. korolkowii	--BG24250	1
E. x macrantha 'The Bride'	87BGN0113	75
E. serratifolia	--BG03409	60
E. tianshanica	85BG35601	71

[a]: accession number of collection in the Botanical Gardens of Wageningen Agricultural University.

[b]: in the Botanical Garden of Chinese Academy of Sciences, Beijing.

7.3.2. Pollinators and their behaviour

Exochorda "species" in Botanical Garden, Institute of Botany, Chinese Academy of Science, Beijing were found to be insect-pollinated. In all, 17 insect species were observed making visits (Table 7.3). The most frequently seen pollinators of *Exochorda* are *Apis cerana* Fabr. (honeybee), constituting 92% of all pollinator species (Table 7.3).

Biotic pollination is a two-sided system, both the blossom and the visitor always depend on external circumstances. Environmental factors such as temperature, sunshine, direction of the wind, relative humidity and altitude have an influence on plant and animal relations. The activity spectrum of pollinators is an important factor in biotic pollination. Vectors depend on meteorologic parameters: below a certain temperature, in a strong wind, or heavy rain, they are inactive. Usually the level of activity rises with temperature until an optimum of environments conditions is reached (Fægri & van der Pijl, 1979).

During the observation from 8:00-10:00 a.m. on April 24, 1996, there was a gale and little sunshine. It was found that there were few insects and only one visit every 15 min. (only *Apis cerana* Fabr. and *Syrphus* spp.). After 10:00 a.m., the weather cleared up and the visits increased.

In Qixia Shan Mt., Nanjing, Jiangsu province of China, *Exochorda* constitutes the second layer of forest, the first layer is *Pinus massoniana* Lamb. There is little sunshine in the forest and only a few pollinators visit the flowers, such as bees and flies. The main pollinators here are *Ceratopogonidae, Anthomyiidae* and *Syrphus* spp.. During a one-day observation in Taibai Shan Mt., Shaanxi province of China, pollinators were rare, caused by altitude (1100 m) and weather. This presumably also led to a low fruit set (<10%) in this population in 1995.

Table 7.3 [a]. Pollinators of *Exochorda*, their body size and hair-cover

Order	Family	Species	L[b]	W[c]	Hair cover
Coleoptera	Cleridae	Unknown	4	2	sparse hair
	Coccinellidae	*Coccinella septempunctata* L.	6	6	sparse short hair
		Leis axyridis (Pallas)	6	6	sparse short hair
	Cetoniidae	*Oxycetonia jucunda* Fald.	13	7	sparse hair
	Scarabaeidae	Unknown	11	7	sparse hair
Diptera	Anthomyiida	Unknown	8	3	sparse hair
	Ceratopogonidae	Unknown	4	1	sparse hair
	Syrphidae	*Syrphus* spp.	12	4	sparse hair
Hemiptera	Reduviidae	*Haematoloecha nigrorufa* (Stål)	12	4	dense short hair
Hymenoptera	Apidae	*Apis cerana* Fabr.	12	5	dense hair
	Bombidae	*Bombus speciosus* Smith	26	10	dense long hair
	Formicidae	Unknown	4	3	sparse hair
	Xylocopidae	*Xylocopa* spp.	21	9	dense long hair
Papilionidae	Lycaenidae	*Rapala caerulea* Bremer & Greg.	15	4	dense short hair
		Satyrium tengstroemi Erschoff	16	5	dense short hair
		Satyrium w-album Knoch	12	4	dense short hair
	Pieridae	*Pieris rapae* L.	17	4	dense long air

[a]: pollinators collected in Botanical Garden, Chinese Academy of Sciences, Beijing in April 1996. L[b]: body length of insect (mm). W[c]: thorax width of insect (mm).

Table 7.4. Percentage of main pollinators to total number of visits during the observations

Pollinator	Total number	Percentage (%)
Apis cerana	305	92
Bombus speciosus	2	0.7
Haematoloecha nigrorufa	1	0.3
Oxycetonica jucunda	1	0.3
Pieris rapae	3	1
Rapala caerulea	10	3.3
Satyrium tengstroemi	3	1
Satyrium w-album	1	0.3
Syrphus spp.	2	0.7
Xylocopa spp.	1	1
Anthomyiidae	3	<1

Bees are the most common visitors and major pollinators of *Exochorda*. The bees land on the corolla or grasp pollen with their legs and thrust their tongues into the nectar disk or pollen. They usually visit some flowers (3.6±1.1) on a plant; movement between flowers is made by a short flight (13.5±0.9 s) or by crawling. As a bee moves around the inflorescence the tongue and legs make contact with the anthers and stigmata of other flowers. Bees collect pollen with the hind pair of legs. This behaviour probably results in cross-pollination when the bees visit other plants. Bees' movements effect pollination by brushing up pollen and depositing pollen grains on stigmata. Bees forage for pollen and nectar on *Exochorda* as a nutritive source.

Most pollinators begin their activities after sunrise and stop activities after sunset. The number of insects increased rapidly after 8:00 a.m. and reached the maximum during 10:00-16:00 (Fig. 7.1). This variation was related to the weather and flowering of *Exochorda*.

Some pollinators also visited other plants in the same community. Pollinators travel to the next inflorescence, returning perhaps to the first one later. The behaviour of pollinators increases the chances of cross-pollination.

Table 7.5. Pollination behaviour of pollinator's visits to *Exochorda*

Pollinator Species	Number of visited flowers	Average visiting time per flower (s)	Average flight between two flowers(cm)
Apis cerana	3.6±1.1	6.5±1.0	13.5±0.9
Pieris rapae	2.4±0.4	25.4±0.4	57.0±0.4
Rapala caerulea	1.6±0.3	53.3±0.7	41.4±0.4
Syrphus spp.	3.7±0.7	8.3±1.1	8.3±1.1

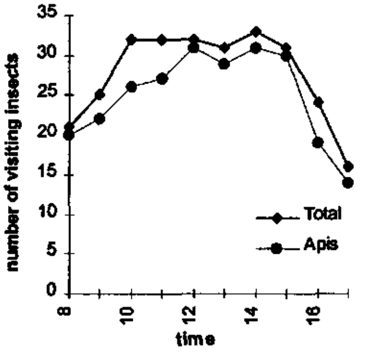

Figure 7.1. Daily variation of pollinator's visit recorded in 15 min at a 1 h interval (April 27, 1996). X: time; Y: the number of visiting insects; Apis: the number of visiting *Apis cerana*; Total: the number of total visiting insects.

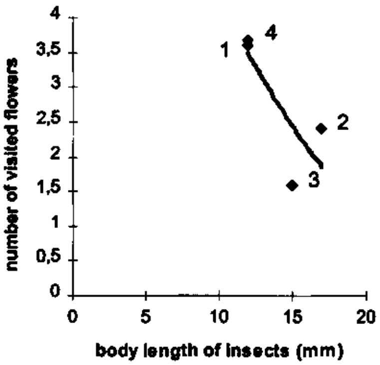

Figure 7.2. The relationship between body length of insects and number of visited flowers. 1: *Apis cerana*; 2: *Pieris rapae*; 3: *Rapala caerulea*; 4: *Syrphus* spp.

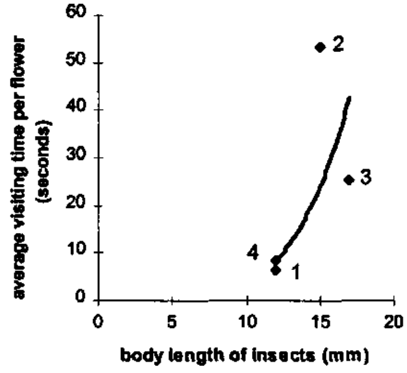

Figure 7.3. The relationship between body length of insects and average visited time per flower. 1, 2, 3, 4: Insect species (as above).

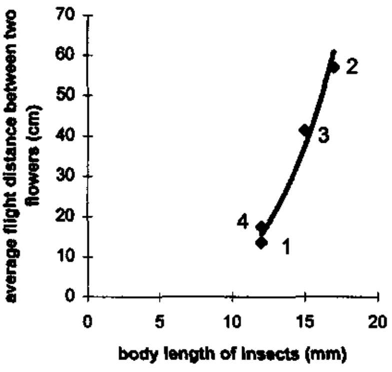

Figure 7.4. The relationship between body length of insects and average flight distance between two flowers.
1, 2, 3, 4: Insect species (as above).

Figure 7.2 shows that the body length of insects is in inverse proportion to the number of visited flowers. The larger the insect, the lower the number of visited flowers. Figure 7.3 and Fig. 7.4 show that the body length of insects is in relatively direct proportion to the average distance of the visit per flower and average flight distance between two visited flowers. The larger the insect, the longer the average visiting time per flower and the average flight distance between two visited flowers.

Apis cerana with shorter body length (12 mm) visited 3.6 (±1.1) flowers every time and flew 6.5 (±1.0) cm from this flower to other one. *Rapala caerulea* with larger body (15 mm) visited 2.4 (±0.4) flowers every time and flew 53.3 (±0.7) cm. Although the butterfly visited fewer flowers, it made longer flight distances. This behaviour plays an important role in long-range exchange of genes in the populations.

7.3.3. Fruit set

During the early period of flowering time, the percentage of well-developed flowers was calculated (Table 7.6). Fruit set in 1996 was 64%, 70%, 54%, 11%, 60%, 27% and 44% for different *Exochorda* "species". And not all of the flowers develop fruit. In general, the last formed 1 to 2 flowers of an inflorescence do not develop a pistil. Or when the topmost flower opens, the preceding 2 to 3 flowers will wilt.

Table 7.6. Fruit set based on different treatments in 1996 and 1997

Species and coll. no.		Control	Treat.1		Treat.2		Treat.3	
		Fr(%)	Fls	Fr(%)	Fls	Fr(%)	Fls	Fr(%)
E. giraldii		64	54	0				
E. racemosa		70	46	0				
E. serratifolia		54	48	0				
E. giraldii	--BG23209	11	27	4	14	7	20	35
E. korolkowii	--BG24250	60	65	59	15	40	26	58
E. x macrantha 'The Bride'	87BGN0113	27	38	24	18	44	16	50
E. tianshanica	85BG35601	44	71	14	21	24	14	50

Control: natural fruit set (at least 50 flowers); Fls: flower; Fr: fruit set; Treat.1-3: see 7.2.4.

7.4. Discussion and conclusions

As in several members of the genus *Prunus* (Sutherland & Delph, 1984), *Exochorda* produces a high proportion of excess flowers and has low fruit set level. Although the present results cannot provide a complete explanation for this phenomenon, several important conclusions can be drawn.

Pollen reaches the stigma by transfer and an attraction mechanism to insect exists. *Exochorda* attracts insects by appearance and odour and shape of the flowers, resulting in transfer of pollen. The inflorescence has more attraction than a single flower (Spira, 1980) and the plant can offer a long period for visiting by a sequential maturation of the flowers. Most saucer-shaped flowers of *Exochorda* are placed on the

the periphery, and the effective area of inflorescence is increased. The pure white corolla attracts beetles, bees, moths and other insects. The large diameter of the corolla allows large and small insects to land on the corolla, this leads to more kinds of pollinators. Pollen and nectar are the rewards for the insect.

Over 30% pistils degenerate (BG24250 is an exception) during the flowering period, leading to low fruit set.

Exochorda flowers from April to May, namely, after the forest canopies are closed and exchange of pollen is hindered. From the observation in different populations in the field, it was recorded that *Exochorda* has a rather low fruit set, especially in populations 01, 02, 07, 10, 14, 15 and 16. In population 14 (Jigong Shan Mt., Henan province, China), there were no flowers and old fruits at all during the survey of 1995, because this population is under deciduous broad-leaved forest and there was a dense forest canopy. It can be concluded that light is an important factor for flower development of *Exochorda.* Population 15 (Taibai Shan Mt., Shaanxi province, China, alt. 1020 m) and population 16 (Taibai Shan Mt., Shaanxi province, China, alt. 1100 m) also occur under forest, and it was found there were few flowers and fruit set was low during the survey of 1995, because of density of forest and high altitude, likely to reduce the chance for pollination by insects.

Apparently the most important groups for pollination are the bees. Their relative abundance on the flowers and their intrafloral behaviour make them a major contributor to the reproductive success of *Exochorda.* Furthermore, the well-known constancy of the social bees (*Apis* and *Bombus*) would enhance their effectiveness as pollinators. Those insects carrying little pollen, had hard hairs on their bodies (such as beetles), or had long legs, or did not alight, and only came into contact with pollen with their legs or proboscises (moths). From the standpoint of the amount of pollen picked up per individual, bees would be much better pollinators than other insects. Other species in non-bee families are also reported as pollinators.

The fruit set of different *Exochorda* accessions varied considerably (Table 7.6). The different factors responsible for these fruit set interact and display spatiotemporal variation. As shown in Table 7.6, after treatment 1 was applied, the fruit set of three "species" in Beijing is 0% in 1996. The reason could be: because temperature and humidity inside the bags rose to high levels. Cross-pollination increases fruit set in most plants, and cross-pollination by humans enhance the efficiency of pollination. There is no self-pollination barrier in different "species". Pollinator diversity and long-range exchange of genes in different populations can result in the blurring of the species boundaries and obscure the morphological difference between genotypes or "species".

Phylogenetic experience indicates that cross-fertilization, outbreeding, has some positive selective value, and there seems to be a general consensus of opinion that this positive value is based on the greater genetic variability produced by genetic recombination in heterozygotic individuals by crossing on the species level (Stebbins, 1957).

Exochorda has a mixed mating system, viz. inbreeding and outbreeding, and >7% of its progeny result from self-pollination (see Table 7.6). Self-pollination plays a secondary role to entomophily.

8. Genetic segregation of random amplified polymorphic DNA in some genera of Rosaceae

8.1. Introduction

As one of the economically most important families of flowering plants, Rosaceae have been well studied systematically. Several classifications have been proposed (Hutchinson, 1964; Robertson, 1974; Yu, 1977; Takhtajan, 1987; Kalkman, 1988; Morgan, 1994). Many authors also studied some taxa belonging to Rosaceae for different purposes.

The taxonomy of *Exochorda* is puzzling because of the similar morphological characters and the lack of clear morphological differences between closely related species. *Exochorda* is included traditionally in the subfamily Spiraeoideae (Yu, 1977; Heywood, 1979). Because of its capsular fruits, it is especially problematic.

With the advent of molecular techniques, DNA-based approaches have been proposed to generate genetic fingerprinting of numerous organisms (Botstein et al., 1980). A very common procedure has been DNA restriction fragment length polymorphism (RFLP). Although RFLP markers are capable of revealing a very large proportion of the existing DNA sequence variation, the analytical process is labour intensive, requires relatively large amounts of tissue, and special facilities for isotope handling.

Williams et al. (1990) reported a novel DNA analysis technique based on the amplification of random DNA sequences using the polymerase chain reaction (PCR) and single primers of arbitrary sequences (usually 10 nucleotides long). This technique has been called, among other acronyms, random amplified polymorphic DNA (RAPD) (Williams et al., 1990) and arbitrarily primed polymerase chain reaction (AP-PCR: Welsh et al., 1991). It is used in numerous organisms to construct detailed genetic studies (Waugh & Powell, 1992). RAPDs are useful both at the intraspecies level and intrafamilial level in some families to evaluate relationships among taxa.

The aim of this phylogenetic study in Rosaceae (especially in *Exochorda*) using RAPD is: 1: assessment of the circumscription and relationships of *Exochorda* in different populations; 2: clarification of the alliances of *Exochorda* in Rosaceae.

8.2. Materials and methods

8.2.1. Plant materials

A total of 26 samples represented a selection of the four subfamilies in Rosaceae. In all, 16 samples of *Exochorda* including wild and cultivated collections were investigated. Sources of plant materials for RAPD are listed in Table 8.1. Total DNA was extracted from silica gel dried leaves or herbarium specimens.

Table 8.1. Sources of plant materials and voucher information for taxa sequenced for RAPD investigation

No.	(Subfamily) Species	Sources and vouchers
	Spiraeoideae	
1	*Sibiraea laevigata* (L.) Maxim.	Cult. in BAC* Gao 0137
2	*Sorbaria kirilowii* (A. Regel) Maxim.	Cult. in BAC Gao 0138
3	*Physocarpus amurensis* (Maxim.) Maxim.	Maoer Shan Mt., Heilongjiang, China
4	*Exochorda racemosa* (Lindl.) Rehder	Pop. 03 Gao 0056
5	*Exochorda racemosa* (Lindl.) Rehder	Pop. 04 Gao 0062
6	*Exochorda racemosa* (Lindl.) Rehder	Pop. 05 Gao 0063
7	*Exochorda racemosa* (Lindl.) Rehder	Pop. 03 Gao 0061
8	*Exochorda racemosa* (Lindl.) Rehder	Pop. 08 Gao 0079
9	*Exochorda racemosa* (Lindl.) Rehder	Pop. 09 Gao 0068
10	*Exochorda racemosa* (Lindl.) Rehder	Pop. 12 Gao 0073
11	*Exochorda racemosa* (Lindl.) Rehder	Pop. 14 Gao 0076
12	*Exochorda giraldii* Hesse	Pop. 15 Gao 0077
13	*Exochorda serratifolia* S. Moore	Pop. 19 Gao 0083
14	*Exochorda serratifolia* S. Moore	Pop. 21 Gao 0086
15	*Exochorda korolkowii* Lavallée	--BG22549 J.v. Veld. 1442 WAU
16	*Exochorda tianschanica* Gontsch.	85BG35601 J.v. Veld. 1436 WAU
17	*Exochorda x macrantha* (Lemoine) C.K. Schneid. 'The Bride'	85BGN3204 J.v. Veld. 1438 WAU
18	*Exochorda racemosa* (Lindl.) Rehder	84BG03409 J.v. Veld. 1432 WAU
19	*Exochorda racemosa* (Lindl.) Rehder	--BG23206 Gao 0017 WAU
	Maloideae	
20	*Cotoneaster hupehensis* Rehder & Wils.	Cult. in BPG*
21	*Sorbus alnifolia* (Sieb. & Zucc.) K. Koch	Cult. in Xiongyue, Liaoning. Gao 0128
22	*Malus micromalus* Makino	Cult. in BAC
	Rosoideae	
23	*Kerria japonica* (L.) DC. f. *pleniflora* (Witte) Rehder	Cult. in BAC
24	*Potentilla parvifolia* Fisch.	Baihua Shan Mt., Beijing. Gao 0133
	Prunoideae	
25	*Prinsepia utilis* Royle	Cult. in Xiongyue, Liaoning Prov.
26	*Amygdalus davidiana* (Carr.) C. de Vos ex Henry	Baihua Shan Mt., Beijing. Gao 0125

*Abbreviations used:
Cult.-cultivated; BAC-Beijing Agricultural College, Beijing; BPG-Chinese Academy of Science, Beijing Plant Garden; WAU-Wageningen Agricultural University, the Netherlands.

8.2.2. DNA isolation

Total DNA was extracted from each individual via phenol/chloroform (1:1) method.

1. Preheat buffer "S" (100 mM 0.1 M Tris.Cl, pH 8.5; 100 mM 0.1 M NaCl; 50 mM 0.05 M EDTA, pH 8.0; 2% SDS) in a water bath (65° C).
2. Grind 0.5-1.0 g dry leaves in a mortar and pestle. The powder is transferred to a 50 ml polypropylene tube.
3. Add 20 mls buffer "S" to polypropylene tube. Mix gently by inversion.
4. Incubate at 65° C for 1-2 h with occasional gentle inversion to mix tube contents.
5. Add 20 mls phenol/chloroform (1:1) to each tube, mix gently by inversion to form an emulsion. Make sure the samples are completely mixed.
6. Centrifuge 4000 rpm (15 min) in bench-top centrifuge to separate phases at room temperature.
7. Remove the acquous phase to a 50 ml centrifuge tube, add 1 volume chloroform, mix gently, centrifuge 4000 rpm (15 min).
8. Remove the acquous phase, add 0.6 vol isopropanol and mix by inversion. Spool out the precipitate with a glass hook, and rinse in an excess of 70% ethanol and air dry briefly on hook (1 h).
9. Dissolve in 5 ml 1×TE.
10. Add 10 ml Rnase stock, and incubate at 37° C for 3-4 h.
11. Phenol/chloroform extract: add 5 ml phenol/chloroform, mix gently by inversion and centrifuge at 4000 rpm for 15 min.
12. Chloroform extract with an equal volume of chloroform.
13. Add 1/10 volume 3 M sodium acetate, mix, and then 2 volumes of cold 95% ethanol.
14. Spool out DNA on glass hook, rinse 2-3 times with 70% ethanol, and air dry one day.
15. Add 1×TE (depending on size of DNA pellet) and allow DNA to dissolve.
16. Measure DNA content by Pharmacia LKB. Ultrospec III and check size by running a small amount through an agarose gel.
17. Samples are stored at 4° C for use.

8.2.3. Primers

DNA primers, 10 nucleotides long, were obtained from Operon Technologies Inc. and are listed in Table 8.2.

Table 8.2. Name and sequence of the DNA primers tested for this study

Name	Sequence (5'-3')	Name	Sequence (5'-3')
OPB-03	CATCCCCCTG	OPO-04	AAGTCCGCTC
OPE-16	GGTGACTGTG	OPO-12	CAGTGCTGTG
OPH-19	CTGACCAGCC	OPO-15	TGGCGTCCTT
OPK-01	CATTCGAGCC	OPO-16	TCGGCGGTTC
OPK-02	GTCTCCGCAA	OPO-20	ACACACGCTG
OPK-04	CCGCCCAAAC	OPX-19	TGGCAAGGCA
OPK-12	TGGCCCTCAC	OPY-02	CATCGCCGCA
OPO-02	ACGTAGCGTC	OPY-18	GTGGAGTCAG
OPO-03	CTGTTGCTAC	OPZ-03	CAGCACCGCA

8.2.4. PCR analysis and electrophoresis

Samples of genomic DNA were used as a template for polymerase chain reaction (PCR) amplification. DNA polymerase in a final mixture volume of 20 μl, contained: 13 μl super H_2O; 2 μl buffer; 0.8 μl dNTP; 0.2 μl Taq; 1 μl primer; 3 μl DNA (30 ng template DNA). The mixture was covered with 20 μl mineral oil. Amplifications were performed with a Programmable Thermal Controller (MJ Research Inc. PTC-100), with a thermal reactor programmed as follows: hot start at 94° C for 2 min; 94° C for 35 s (denaturing); 36° C for 15 s (annealing); 72° C for 45 s (extension) (46 cycles), final elongation at 72° C for 4 min and subsequent cooling down to 4° C.

DNA amplification products with 5 μl were electrophoresed in 1.4% agarose gel at 70 V in TAE buffer for 5 h to separate amplified bands and stained with EB (ethidium bromide). A Hae III digest DNA marker was loaded on each gel to assess band size. Gels were visualized under UV light and photographed on Kodak film.

8.2.5. Data analysis

Allele frequencies were used to calculate genetic distance between all samples. The resulting distance matrix was then used to construct a phenetic tree of different samples. PCR-amplification products (=bands) were identified by eye and were listed as discrete characters per sample. Individual DNA bands were scored as present (1) or absent (0) in the amplification profile of each line. Each DNA band represents a locus having a dominant allele (presence of the DNA band) and a recessive allele (absence of the DNA band). Only clear DNA bands were scored and primers that did not amplify more plants were discarded. The band sharing among the samples was calculated using the equation: $D = (2nAB/nA+nB)\times 100$, where nA is the number of bands in plant A, nB is the number of bands in plant B and nAB is the number of bands shared between A and B. The D score for each pair with all selected primers was then calculated. Data analysis was performed with NTSYS-pc, version 1.80 (Rohlf, 1993).

8.3. Results and discussion

In total, 50 primers were surveyed for this analysis, and 18 of these primers were found to be suitable for this investigation, the other primers produced poor or no amplification products. Each primer produced different amplification product patterns. The number of bands detected using 18 primers ranged from 1 to 9. All the bands revealed by 18 arbitary primers were polymorphic. Product sizes typically ranged between approximately 0.4 to 2.0 kb.

Reactions performed in the presence of primer OPK12 resulted in the amplification of all 26 samples. Figure 8.1 shows the RAPD phenotypes of 26 samples following amplification with premier OPK12. Polymorphism were detected. For example, the banding pattern for sample 4 (*Exochorda* spp.) using primer OPK12 was identical to that for sample 5, 6 and 7 (*Exochorda* spp.), and was different from the patterns of the other samples.

It is notable that the banding pattern using primer OPX19 was shared by all *Exochorda* samples and was markedly different from other samples (data not shown).

Figure 8.1. DNA polymorphisms generated by primer OPK12 among 26 samples. The numbers 1-26 refer to the samples listed in Table 8.1.

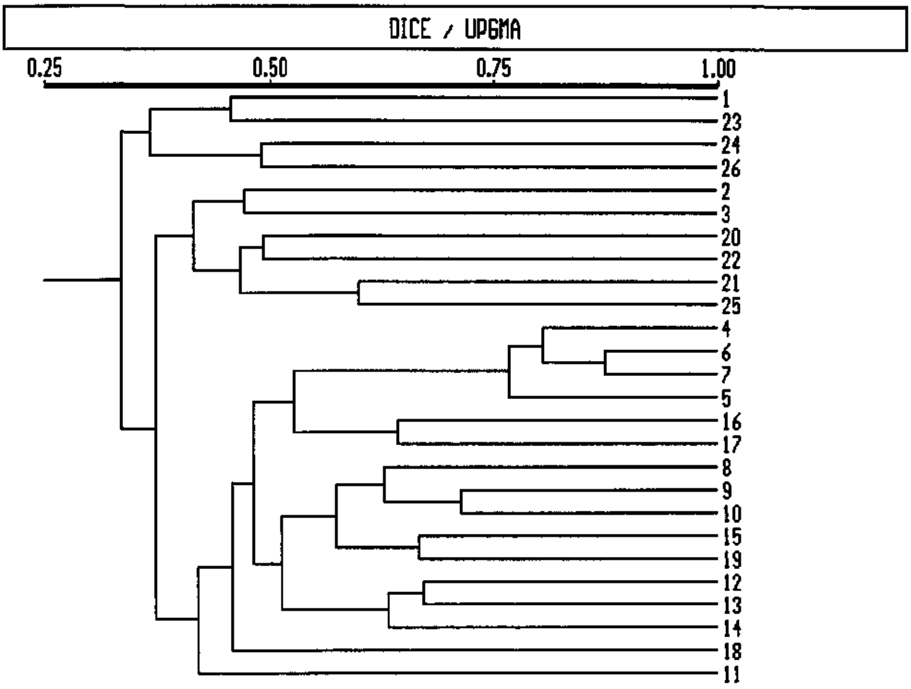

Figure 8.2. Dendrogram of 26 samples of Rosaceae generated by UPGMA.
The numbers 1-26 are explained in Table 8.1.

Cluster analysis using similarity defined three broadly groups of samples (Fig. 8.2). From the RAPD results in some Rosaceae, it is concluded that five previously distinguished taxa (five species) of *Exochorda* are not distinct. Instead, all *Exochorda* samples were defined in one group and are distinct from other genera in Rosaceae, i.e. it does not show five previously described taxa (five species) in the *Exochorda* complex.

Within the *Exochorda* complex, the closest group includes populations 03, 04, 05 and Gao 0061 under the name *E. racemosa*, occurring in East China. Two other cultivated samples 85BG35601 under the name *E. tianschanica* and 85BGN3204 under the name *E. x macrantha* 'The Bride' are also grouped in this phenon. Another group includes different populations under the name *E. korolkowii*, *E. racemosa*, *E. giraldii* and *E. serratifolia*. Samples 84BG03409 and population 14 are not closely associated with these groups.

As far as the phenogram is concerned, the *Exochorda* samples are different to interpret as different species because of the lack of distinction. Moreover, samples from the same "species" collected in the same region were grouped with other "species". The molecular data indicate that the interspecific relationships of *Exochorda* are less clear, the genetic segregation of random amplified polymorphic DNA among the genus is weak. Combined with DNA content (Chapter 5), it can be concluded that there is little difference within the genus *Exochorda*.

The second group is composed of samples from subfamilies Spiraeoideae, Rosoideae and Prunoideae, another group is composed of samples from Spiraeoideae, Maloideae and Prunoideae. This result is not in accordance with the previous subfamily taxa interpretation. Results from this study suggest that based on RAPD data not all the samples from the same subfamily are to be closed in one group. Although the material is limited, it indicates some relationships in the family. The RAPD data also disturb the common opinion regarding the traditional subfamily taxa in Rosaceae. The four subfamilies as separate taxonomic units in Rosaceae are quite heterogeneous. Are they really natural groups?

I was not able to distinguish *Exochorda* into five taxa, one broad group was defined. This result is in accordance with the results using traditional means (see earlier chapters). We suggest that PCR based on RAPD is a rapid and reliable method. Additionally, analysis of RAPD patterns should prove useful in indicating relationships between *Exochorda* and other groups in the family Rosaceae.

9. Multivariate analysis of morphological variation in the *Exochorda* complex

9.1. Introduction

The *Exochorda* complex consists of five officially published species (Index Kewensis). Three "species" are distributed in China and the Korean peninsula, and others in Kirghizstan, Tadzhikistan, Turkestan and Uzbekistan (see Chapter 11). However, there is a strong morphological resemblance between these taxa, showing more or less overlapping variations in many characters. Pollen analysis of 33 *Exochorda* accessions indicates a close relationship, because pollen shape, exine structure and surface ornamentation are uniform. Furthermore, wood anatomical and chromosome data do not indicate significant differences between the five species (see earlier chapters).

The taxa involved were distinguished (in their protologues) from each other mainly by leaf length, number of stamens, number of flowers per inflorescence and a few other characters. But the careful checking of wild accessions and cultivated specimens revealed that most characters display a continuous variation between species.

It is interesting to note that all the taxa have a restricted distribution and ecological variation. *E. giraldii* is only distributed in Central and Northwest China, *E. serratifolia* is known from Northeast China and the Korean peninsula, *E. racemosa* occurs in East China, while *E. korolkowii* and *E. tianschanica* are found in Kirghizstan, Tadzhikistan, Turkestan and Uzbekistan. Although different approaches were used to distinguish the taxa, multivariate analysis are also an important approach for the delimitation of taxa. In this chapter, we used multivariate techniques to elucidate the variation between *Exochorda* "species" occuring in several geographic regions and to try to obtain a satisfactory classification of the *Exochorda* complex.

9.2. Materials and methods

Herbarium material of twenty-nine accessions of all taxa in the genus *Exochorda* including wild populations and cultivated plants in WAU was examined (Table 9.1). These accessions represented all the "species" that were available from the wild throughout its distribution. In total 40 morphological characters were selected as operational taxonomic units (OTU's) and measured for each population based on 10 measurements (Table 9.2), while leaf and flower characters for flowering specimens, fruit characters for fruiting specimens. But 10 characters were disregarded because no difference existed. Some characters with two (0, 1) or three (0, 1 & 2) character-states have been considered. Quantitative characters were directly measured from the specimens.

Each character was analyzed for its average, standard deviation and CV. The data sets were computed for principal component analysis (PCA) and cluster analyses. All the above calculations were performed with NTSYS-pc, version 1.80 (Rohlf, 1993).

Table 9.1. Origin of materials for numeral taxonomy

No.	Pop.	Voucher specimens	Names in previous classification	Locality
1	Pop. 01	Gao 0051	*E. racemosa* (Lindl.) Rehder	Qixia Shan Mt., Nangjing, Jiangsu
2	Pop. 02	Gao 0052, 0053	*E. racemosa* (Lindl.) Rehder	Chadaokou, Nangjing, Jiangsu
3	Pop. 03	Gao 0056, 0057	*E. racemosa* (Lindl.) Rehder	Lingyan Shan Mt., Suzhou, Jiangsu
4	Pop. 03	Gao 0061	*E. racemosa* (Lindl.) Rehder	Lingyan Shan Mt., Suzhou, Jiangsu
5	Pop. 04	Gao 0062	*E. racemosa* (Lindl.) Rehder	Lingyan Shan Mt., Suzhou, Jiangsu
6	Pop. 05	Gao 0063, 0103	*E. racemosa* (Lindl.) Rehder	Dengwei Shan Mt., Suzhou, Jiangsu
7	Pop. 06	Gao 0064	*E. racemosa* (Lindl.) Rehder	Dengwei Shan Mt., Suzhou, Jiangsu
8	Pop. 07	Gao 0065, 0090	*E. racemosa* (Lindl.) Rehder	Geling Mt., Hangzhou, Zhejiang
9	Pop. 08	Gao 0075	*E. racemosa* (Lindl.) Rehder	Zhongtianmen, Jigong Shan Mt., Henan
10	Pop. 09	Gao 0068, 0105, 0106	*E. racemosa* (Lindl.) Rehder	Baoxiaofeng, Jigong Shan Mt., Henan
11	Pop. 10	Gao 0069, 0070	*E. racemosa* (Lindl.) Rehder	Longzikou, Jigong Shan Mt., Henan
12	Pop. 11	Gao 0071, 0108	*E. racemosa* (Lindl.) Rehder	Longzikou to Doushiya, Jigong Shan Mt., Henan
13	Pop. 12	Gao 0073	*E. racemosa* (Lindl.) Rehder	Doushiya, Jigong Shan Mt., Henan
14	Pop. 13	Gao 0074	*E. racemosa* (Lindl.) Rehder	Xianrenjing, Jigong Shan Mt., Henan
15	Pop. 15	Gao 0077, 0078, 0111	*E. giraldii* Hesse	Heihuguan, Taibai Shan Mt., Shaanxi
16	Pop. 16	Gao 0079, 0109	*E. giraldii* Hesse	Jiaokou, Taibai Shan Mt., Shaanxi
17	Pop. 17	Gao 0080	*E. giraldii* Hesse	Hua Shan Mt., Huayin, Shaanxi
18	Pop. 18	Gao 0081, 0082, 0114	*E. giraldii* Hesse	Shigao Shan Mt., Lingshi, Shanxi
19	Pop. 19	Gao 0083, 0089	*E. serratifolia* S. Moore	Wuling Shan Mt., Xinglong, Hebei
20	Pop. 20	Gao 0085, 0116, 0017	*E. serratifolia* S. Moore	Fenghuang Shan Mt., Chaoyang, Liaoning
21	Pop. 21	Gao 0086, 0119, 0120	*E. serratifolia* S. Moore	Haitang Shan Mt., Fuxin, Liaoning
22	Pop. 22	Gao 0087	*E. serratifolia* S. Moore	Haitang Shan Mt., Fuxin, Liaoning
23			*E. korolkowii* Lavallée	
24			*E. tianschanica* Gontsch.	
25*		--BG23207	*E. giraldii* Hesse	WAU Botanical Gardens
26*		--BG23209	*E. korolkowii* Lavallée	WAU Botanical Gardens
27*		--BG24250	*E. tianschanica* Gontsch.	WAU Botanical Gardens
28*		87BGN0113	*E. x macrantha* (Lemoine) C.K. Schneid. 'The Bride'	WAU Botanical Gardens
29*		--BG23206	*E. racemosa* (Lindl.) Rehder	WAU Botanical Gardens

25*-29*: cult. in the Botanical Gardens, Wageningen Agricultural University, the Netherlands.

Table 9.2. List of OTU's for numerical analysis

OTU's number	Abbreviations	Characters	
1	LL	leaf length (mm)	
2	LW	leaf width (mm)	
3	LL/LW	leaf length/leaf width	
4	NS	number of serrations	
5	POL	petiole length (mm)	
6	LL/POL	ratio: leaf length/petiole length	
7*	CP	colour of petiole	0-greenish; 1-reddish
8*	HUS	hair on upper surface	0-glabrous; 1-dense hairs; 2-sparse hairs
9*	HLS	hair on lower surface	0-glabrous; 1-dense hairs; 2-sparse hairs; 3-hair on versus
10*	HP	hair on petiole	0-glabrous; 1-dense hairs; 2-sparse hairs
11*	AL	apex of leaf	0-obtuses; 1-acutes; 2-mucronates
12*	BL	base of leave	0-cuneates; 1-angustates
13	IL	inflorescence length (mm)	
14	NF	number of flowers per inflorescence	
15	DF	distance between two flowers (mm)	
16	NA	number of anthers	
17	OL	ovary length (mm)	
18	CD	corolla diameter (mm)	
19	LFP	length of flower petiole (mm)	
20	PAL	petal length (mm)	
21	PW	petal width (mm)	
22	PAL/PW	ratio: petal length/petal width	
23	CL	calyx length (mm)	
24	CW	calyx width (mm)	
25	CL/CW	ratio: calyx length/calyx width	
26*	HC	hair on calyx	0-glabrous; 1-dense hairs; 2-sparse hairs
27*	HP	hair on petiole	0-glabrous; 1-dense hairs; 2-sparse hairs
28	FL	fruit length (mm)	
29	FW	fruit width (mm)	
30	FL/FW	ratio: fruit length/fruit width	
31	FPL	fruit petiole length (mm)	
32	SL	seed length (mm)	
33	SW	seed width (mm)	
34	SL/SW	ratio: seed length/seed width	
35*	PS	pollen shape	0-other shapes; 1-spheroidal
36*	OP	ornamentation of pollen	0-others; 1-striate
37*	GRW	growth ring of wood	0-growth ring absent; 1-growth ring present
38*	RPW	ring porosity of wood	0-ring-porous-semi-ring-porous; 1-ring-porous
39*	B	branch	0-branch pendulous; 1-branch erect
40	ML	leaf margin	undulate

Because differences were absent or features were repeated, we deleted characters 2, 5, 17, 21, 24, 29, 33, 35, 36, and 39.

9.3. Results

9.3.1. Character analysis

Variation was observed in a number of qualitative characters. Average values, standard deviation and CV for morphological characters are reported in Table 9.3. CV analysis showed high variation for number of leaf serrations (NS), petiole length (POL), leaf length/petiole length (LL/POL), and length of flower petiole (LFP).

Table 9.3. Average (AVE), standard deviation (STDEV) and CV based on 30 characters

No.	Character	AVE ± STDEV (CV)
1	leaf length (mm)	33.38 ± 5.95 (0.1783)
2	leaf width (mm)	17.58 ± 4.27 (0.2427)
3	ratio: leaf length/leaf width	1.98 ± 0.37 (0.1884)
4	number of serrations	0.91 ± 1.63 (1.7826)
5	petiole length (mm)	6.56 ± 3.69 (0.5625)
6	ratio: leaf length/ petiole length	7.30 ± 4.08 (0.5583)
13	inflorescence length (mm)	71.23 ±12.46 (0.1749)
14	number of flowers per inflorescence	7.02 ± 1.31 (0.1866)
15	distance between two flowers (mm)	10.48 ± 1.85 (0.1767)
16	number of anthers	20.07 ± 5.36 (0.2673)
18	corolla diameter (mm)	36.07 ± 4.68 (0.1296)
19	length of flower petiole (mm)	2.16 ± 1.13 (0.5238)
20	petal length (mm)	17.75 ± 3.61 (0.2033)
21	petal width (mm)	10.54 ± 2.13 (0.2024)
22	ratio: petal length/petal width	1.72 ± 0.31 (0.1795)
23	calyx length (mm)	3.18 ± 0.44 (0.1371)
24	calyx width (mm)	4.09 ± 0.71 (0.1744)
25	ratio: calyx length/calyx width	0.79 ± 0.11 (0.1350)
28	fruit length (mm)	10.25 ± 1.52 (0.1486)
29	fruit width (mm)	11.49 ± 0.90 (0.0785)
30	ratio: fruit length/fruit width	0.90 ± 0.12 (0.1356)
31	fruit petiole length (mm)	3.72 ± 1.43 (0.3848)
32	seed length (mm)	8.40 ± 1.30 (0.1542)
33	seed width (mm)	4.83 ± 0.55 (0.1144)
34	ratio: seed length/seed width	1.75 ± 0.23 (0.1292)

Leaf: Leaf characters were used to distinguish previous taxa in the protologues in the *Exochorda* complex. However, the results for leaf characters analyzed in this chapter show that there is continuous variation in leaf length (LL), leaf width (LW), leaf length/ leaf width (LL/LW) (Figs. 9.1, 2, 3). Vegetable characters are much more related to ecology condition. Leaves in Kirghizstan, Tadzhikistan, Turkestan and Uzbekistan are relative longer and narrower and with a large LL/LW ratio than those in other populations. Leaves in populations 19, 20, 21 & 22 are shorter with a small

LL/LW ratio. Compared with other populations, populations 15, 16, & 17 (Taibai Shan Mt. & Hua Shan Mt., at > 1000 m altitude) were highly variable with large and entire leaves. In a word, within the complex, there is no obvious disjunct variation in LL, LW and LL/LW.

Serration: Serration seems to be good character to distinguish *E. serratifolia* (populations 19, 20, 21 & 22) (Fig. 9.4 showing flowering specimens). The number of serrations in populations 19, 20, 21 and 22 is larger than those in other populations. It is notable that young leaves with sparse serrations are common in other populations, namely serration is not only restricted to *E. serratifolia* (Fig. 9.4), and although in populations 19, 20, 21 and 22 mature leaves have less serrations than young ones.

Hairs: The indumentum is not a reliable character within the complex. Generally speaking, at maturity individual leaves are glabrous, no hairs are extant on both surfaces, or other parts, or very sparse hairs can be seen on both surfaces, on petiole or on pedicels. Only one specimen (Gao 0068) in Jigong Shan Mt. has dense hairs. Hairs often occur on young leaves, young branches and flower pedicels.

Flower, fruit: From the PCA it is concluded that some characters in flower, fruit, seed contribute more to the segregation of those taxa than others. But in most cases there is considerable and continuous overlap of the ranges. Figures 9.5, 6, 7 show flower and stamen characters range in 29 accessions (missing data in BG23206 in flower character). For example, difference in petal shape was small among accessions. Petal length and number of anthers in populations 15, 16, 17 & 18 are larger than those in other populations (Figs. 9.5, 7).

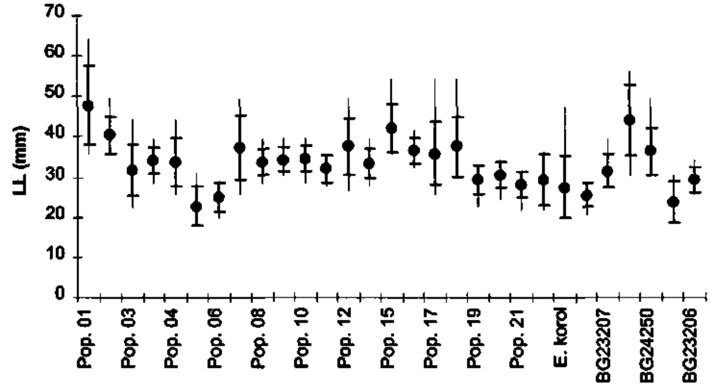

Figure 9.1. Presentation of leaf length variation. X: populations number (see Table 9.1); Y: leaf length (mm); Central symbol • : mean; ——— : range (min., & max.); ⊢——⊣ : standard deviations.

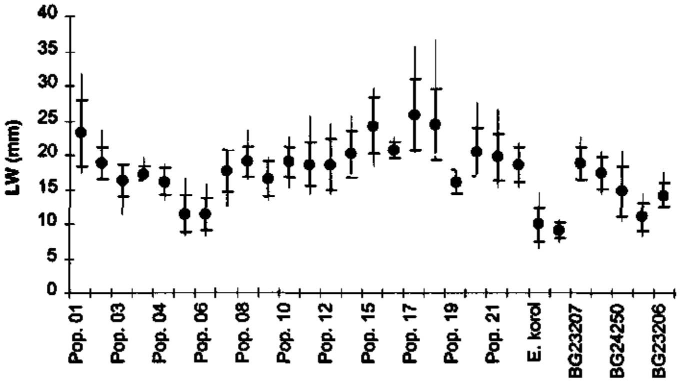

Figure 9.2. Presentation of leaf width variation. X: populations (see Table 9.1); Y: leaf width (mm); Central symbol • : mean; ——— : range (min., & max.); |——|: standard deviations.

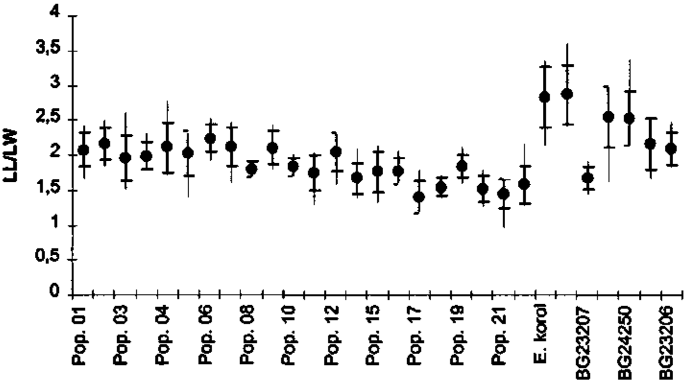

Figure 9.3. Presentation of leaf length/leaf width ratio variation. X: populations (see Table 9.1); Y: ratio (leaf length/leaf width); Central symbol • : mean; ——— : range (min., & max.); |——| : standard deviations.

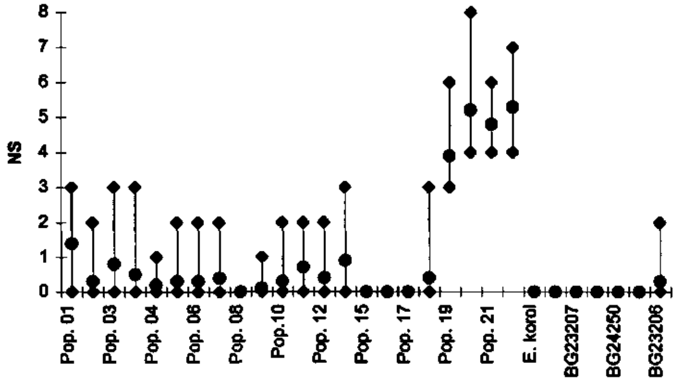

Figure 9.4. Presentation of number of serrations variation. X: populations (see Table 9.1); Y: number of serrations; Central symbol • : mean; ◆——◆: range (min., & max.).

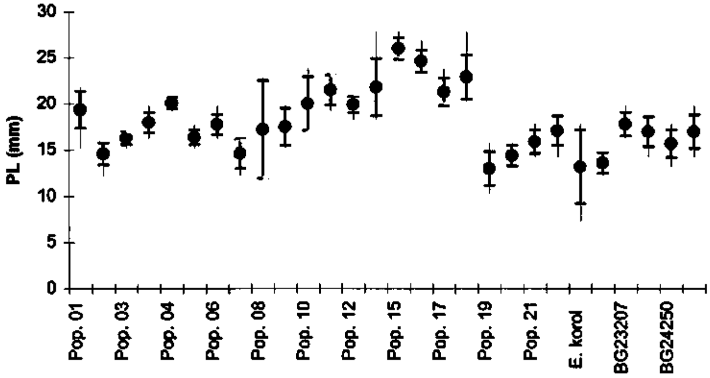

Figure 9.5. Presentation of petal length variation. X: populations (see Table 9.1); Y: petal length (mm); Central symbol • : mean; ——— : range (min., & max.); |——|: standard deviations.

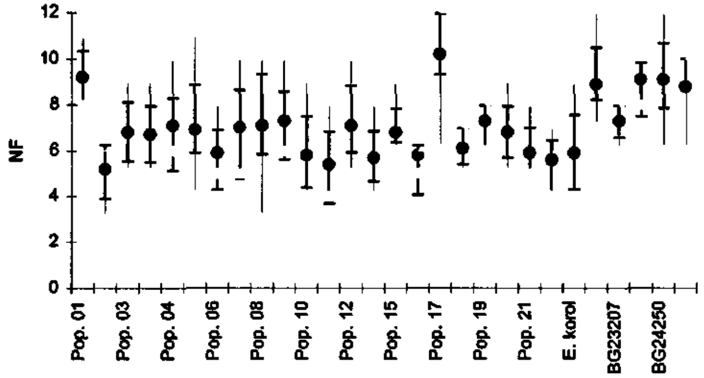

Figure 9.6. Presentation of number of flowers per inflorescence variation. X: populations (see Table 9.1); Y: number of flowers per inflorescence; Central symbol • : mean; ——— : range (min., & max.); |——| : standard deviations.

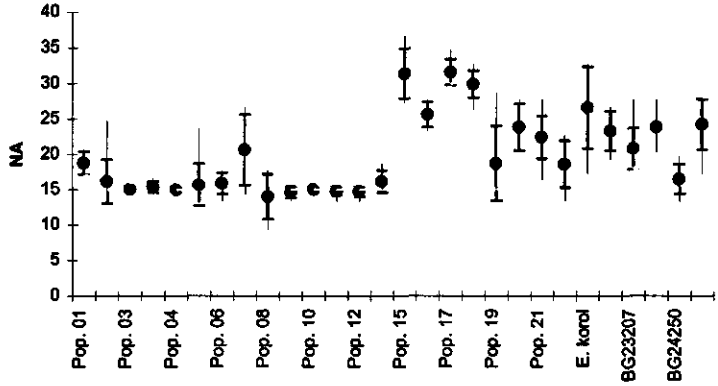

Figure 9.7. Presentation of number of stamens per flower variation. X: populations (see Table 9.1); Y: number of stamens; Central symbol • : mean; ——— : range (min., & max.); |——| : standard deviations.

Seed weight per 1000:

Seed weight (g) per 1000 seeds is listed in Table 9.4. Analysis of variance was used for this study.

Table 9.4. Seed weight (g) from different populations

Previous taxa	*E. racemosa*			*E. giraldii*			*E. serratifolia*		
Locality	1	2	3	4	5	6	7	8	9
Weight (g)	8.28	10.22	11.46	9.48	11.63	9.98	9.44	9.11	7.60

Locality: 1. Lingyan Shan Mt., Pop. 03; 2. Geling Mt., Pop. 07; 3. Baoxiaofeng, Jigong Shan Mt., Pop. 09; 4. Jiaokou, Taibai Shan Mt., Pop. 16; 5. Heiguguan, Taibai Shan Mt., Pop. 15; 6. Shigao Shan Mt., Pop. 18; 7. Wuling Shan Mt., Pop. 19; 8. Fenghuang Shan Mt., Pop. 20; 9. Haitang Shan Mt., Pop. 21. For further explanation, see text.

Table 9.5. Analysis of variance for seed weight

Resource	DF	SS	MS	F
Species	2	44.760	22.380	1.400
Locality/species	6	95.834	15.970	26.620**
RE	81	48.980	0.605	
Total	89	189.574		

DF: degrees of freedom; SS: sum of squares; MS: mean square; F: F-ratio; RE: random error.

Concerning species: $F_{0.05}$ (2, 6) = 5.15, $F < F_{0.05}$; so no significant difference between species.

Concerning different populations within a species: $F_{0.05}$ (6, 81) = 2.21, $F > F_{0.05}$, difference is significant.

Table 9.6. Analysis of variance for seed weight between different localities

Resource	DF	SS	MS	F
Locality	8	140.594	17.574	29.047**
Error	81	48.980	0.605	
Total	89	189.574		

$F = 29.047 > F_{0.01}$ (8, 81) = 2.74, significant difference, so a Q-check (due to J.W. Tukey) was used to compare seed weight between different localities (cf. Snedecor & Cochran, 1980).

Based on number and random error, from q list: $q_{0.05}$ (9, 81) = 4.550, $q_{0.01}$ (9, 81) = 5.360.

$Se = \sqrt{MSe/n} = 0.246$

Significant difference: $D_{0.05} = q_{0.05} \times Se = 4.55 \times 0.246 = 1.119$

$D_{0.01} = q_{0.01} \times Se = 5.36 \times 0.246 = 1.319$

The sequence from large to small of average seed weight (g/1000) in different localities is arranged in Table 9.7. All pairwise differences were compared to $D_{0.05}$ and $D_{0.01}$. If the difference is larger than $D_{0.05}$, then there is a significant difference, denoted by *; if the difference is larger than $D_{0.01}$, the difference is heavily significant **.

Table 9.7. Seed difference between nine different localities

	X_j-X_9	X_j-X_1	X_j-X_8	X_j-X_7	X_j-X_4	X_j-X_6	X_j-X_2	X_j-X_3
X_5=11.63	4.03**	3.35**	2.52**	2.19**	2.15**	1.65**	1.41**	0.17
X_3=11.46	3.86**	3.18**	2.35**	2.02**	1.98**	1.48**	1.24*	
X_2=10.22	2.62**	1.94**	1.11	0.78	0.74	0.24		
X_6=9.98	2.38**	1.70**	0.87	0.54	0.50			
X_4=9.48	1.88**	1.20*	0.37	0.04				
X_7=9.44	1.84**	1.16*	0.33					
X_8=9.11	1.51**	0.83						
X_1=8.28	0.68							
X_9=7.60								

9.3.2. Principal component analysis (PCA)

PCA results using 30 characters are given in Fig. 9.8. PCA shows that all the 29 OTU's formerly cited under five names tend to be roughly grouped in three groups in the scatterplot of PC1 vs. PC2 (Fig. 9.8). For example, one group consists of populations 15, 16, 17 and 18 collected in Northwest and Central China under the name *E. giraldii*; another group is composed of populations 19, 20, 21 and 22 collected in Northeast China under the name *E. serratifolia*. Both groups appear to be distinct from the rest of the taxa in the complex. The largest group consist of accessions cited as *E. racemosa* collected in East China, and *E. korolkowii* and *E. tianschanica* collected in Kirghizstan, Turkestan and Uzbekistan.

The group including populations 15, 16, 17 and 18 can be recognized in the scatterplot of PC1 vs. PC 3 (date not shown) and other collections were merged. The morphological differentiation of "entire leaf" group (i.e. *E. giraldii*) and "serrate leaf" group (*E. serratifolia*) is certainly stronger than that of the "leaf margin entire or rarely serrate above the middle" group (*E. racemosa*).

The total character loadings on the first three PC's are shown in Table 9.9. The first three PC's revealed a total 49% variation messages of the data sets (Table 9.8). The first axis (PC1), describing 21% of the variation, is mainly composed of PAL, FL, SL and DF. The second axis (PC2), describing 15% of the variation, is determined by NS, AL, LL/POL, IL. The third axis, accounting for 13% of the variation, is mainly determined by NF, IL, NA and SL/SW. So the most important characters contributing to the first principal component (PC1) are petal length (PAL) (0.76), fruit length (FL)

(0.74), seed length (SL) (0.72), and distance between two flowers (DF) (0.70). Obviously, the PC1 represents characters on flower, fruit and seed which contribute more to the segregation of those taxa. The most important characters contributing to the second principal component (PC2) are number of serrations (NS) (-0.86), apex of leaf (AL) (0.83), leaf length/petiole length (LL/POL) (0.67), inflorescence length (IL) (0.61). The PC2 represents both leaf and flower characters. For the third principal component (PC3), more contributing characters are number of flowers per inflorescence (NF) (0.70), inflorescence length (IL) (0.63), number of stamens (NA) (0.62) and seed length/seed width ratio (SL/SW) (-0.62) which also represent flower, and seed characters. Most of these characters are weakly diagnostic and are used to distinguish taxa in the complex.

Table 9.8. The first six principal components and percentages

No.	Eigenvalue	Percent	Cumulative
1	6.31	21.03	21.04
2	4.48	14.93	35.97
3	4.02	13.40	49.36
4	2.88	9.60	58.96
5	2.53	8.44	67.40
6	1.59	5.29	72.69

Table 9.9. Character loadings on first three PC's in PCA

Character	PC1	PC2	PC3	Character	PC1	PC2	PC3
1	0.25	0.45	0.36	19	0.57	0.46	0.37
3	-0.51	0.46	-0.22	20	0.76	0.34	0.27
4	-0.12	-0.86	0.10	22	0.25	0.22	-0.08
6	-0.43	0.67	-0.17	23	0.15	0.35	0.14
7	0.66	0.10	0.48	25	-0.60	0.34	0.16
8	0.54	-0.11	0.32	26	0.16	0.17	-0.22
9	0.66	-0.15	0.40	27	0.16	0.17	-0.22
10	0.33	0.12	-0.08	28	0.74	0.12	-0.54
11	0.00	0.83	-0.13	30	0.48	0.21	-0.56
12	-0.24	0.38	-0.35	31	-0.49	0.43	-0.29
13	0.23	0.61	0.63	32	0.72	0.04	-0.53
14	-0.47	0.36	0.70	34	0.51	0.33	-0.62
15	0.70	0.25	-0.05	38	0.24	-0.54	-0.31
16	0.39	-0.15	0.62	39	-0.21	0.02	0.31
18	0.57	0.46	0.37	40	-0.22	0.13	-0.06

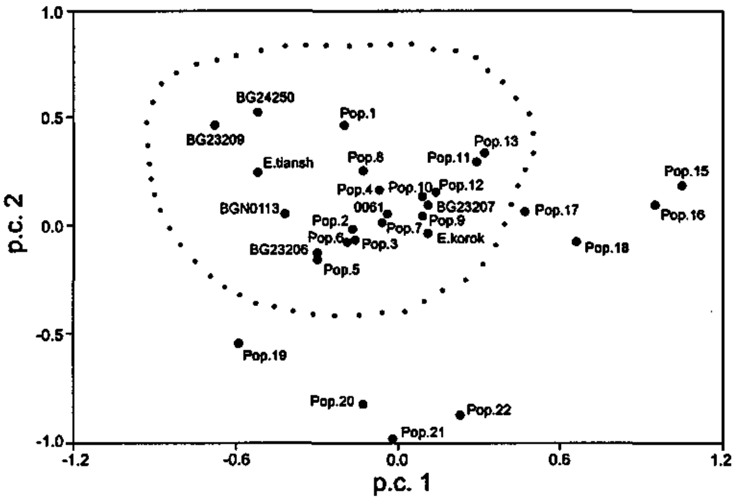

Figure 9.8. Principal component plot of 29 *Exochorda* accessions based on 30 morphological characters.

9.3.3. Phenetic analysis

The phenetic dendrogram (Fig. 9.9) using similarity clustered by UPGMA indicates that the 29 OTU's can be divided into 4 phenons. The largest group consists of most OTU's cited under different species names as *E. racemosa*, *E. korolkowii* and *E. tianschanica* which are collected respectively from East China, Kirghizstan, Tadzhikistan, Turkestan and Uzbekistan. This group represents the morphological characters including "leaf glabrous, sparsely serrate above the middle". It is noteworthy that all the collections from Botanical Gardens of Wageningen Agricultural University under different species names as *E. racemosa*, *E. korolkowii*, *E. giraldii*, *E. serratifolia*, *E. tianschanica* and *E. x macrantha* 'The Bride' are all grouped in this phenon. One *E. serratifolia* population (Pop. 19) resembled *E. racemosa*. Another phenon is composed of 3 populations of *E. serratifolia* which consists of "serrate leaf" group from Northeast China. The last group consists of *E. giraldii* which consists of "entire leaf" group collected from Northwest and Central China. One *E. racemosa* population (Pop. 13) is also included in this group, and obviously constitutes the extreme variants of *E. racemosa*. Figure 9.9 also shows that the "serrate leaf" group, "leaf entire with long petiole" group and the group with "leaf margin entire or rarely serrate above the middle" are distinct from each other.

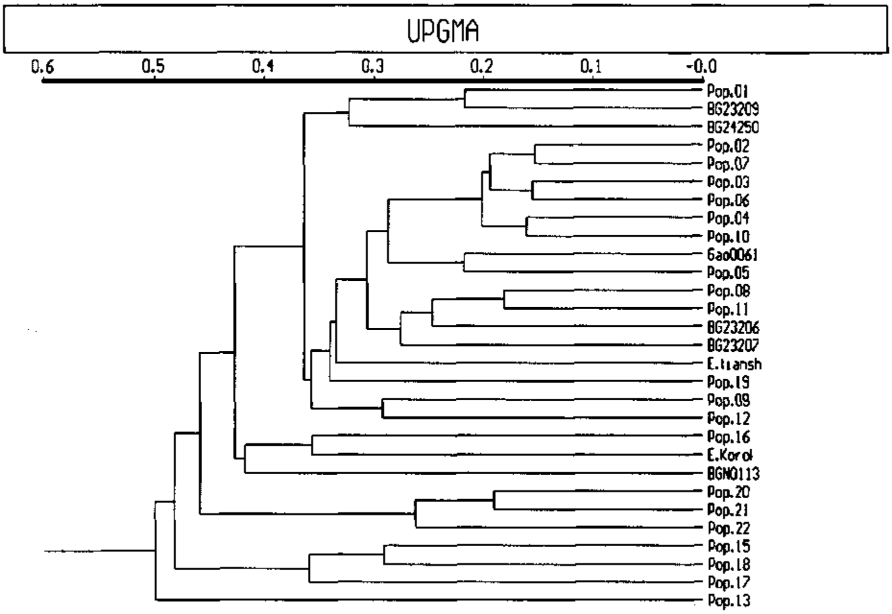

Figure 9.9. Phenogram of 29 populations of *Exochorda* complex based on 30 characters.

9.4. Discussion

Based on their protologues, most of the determinative features are quantitative and actual values of individual characters may vary significantly and overlap. Morphological characters considered in identification of previous taxa are numbers of stamens, colour of petiole and hairiness of leaf. We have found that all of these characters are highly variable within populations and thus not reliable. The number of stamens in every population is also variable. Colour of petiole and hairiness of leaf depends both on environmental conditions and on leaf ontogenesis. Young leaves have more or less reddish petioles and hairiness. Sometimes leaf size was used to separate different taxa. This character is also related to climatic conditions.

The findings in this chapter point to a continuous variation of morphological characters. This analysis supports the opinion that overall morphological difference is small within the *Exochorda* complex. Morphological characters such as petiole length, fruit length, seed length, number of serration, apex of leaf, leaf length/petiole length ratio, number of flowers per inflorescence, inflorescence length and number of stamens were found to be important for distinguishing groups.

The multivariate analysis results do not support five distinct taxa (i.e. previous classification - five species) in the *Exochorda* complex. Instead, three broadly defined taxa can be recognized. These coincide in part with the geographical distributions in the genus. Populations 15, 16, 17 and 18 are related, representing "leaf glabrous with long petiole" under the name *E. giraldii* and distributed in Northwest and Central China. These populations are limited to elevations between 900 to 1200 m. Populations 19, 20, 21 and 22 are related showing "leaf serrate" character and are confined to Northeast China under the name *E. serratifolia*. Others belong to one large closely related group including *E. racemosa, E. korolkowii* and *E. tianschanica*. The final group is composed of the populations from East China and Kirghizstan, Tadzhikistan, Turkestan and Uzbekistan. Apparently, the distinction between *E. racemosa, E. korolkowii* and *E. tianschanica* is not clear based on observed morphological characters.

Because of a series of widely overlapping characters, the complex of the Central Asian *E. korolkowii* and *E. tianshanica* is closely related to and grouped with the complex of the Chinese *E. racemosa* in the PCA (Fig. 9.8) and UPGMA (Fig. 9.9). Morphologically they are very similar, although their distribution is distinctly disjunct (the reason will be discussed in Chapter 11). The morphological and geographical separation between the populations from Kirghizstan, Tadzhikistan, Turkestan and Uzbekistan is weak, the classification based on few characters for the two Central Asian "species" is untenable. *E. korolkowii, E. tianshanica* and *E. racemosa* appear conspecific. *E. korolkowii* and *E. tianshanica* will be united with *E. racemosa* and treated as synonyms.

Although the phenetic analysis places the populations into taxonomically relevant groups, there is some discrepancy with the PCA. For example, population 19 from Wuling Shan Mt. (Northeast China) was placed with the group from East China in the phenetic analysis, while population 13 from Jigong Shan Mt. was not grouped with them together. PCA grouped all cultivated samples (Cult. in WAU) under different names with *E. racemosa*. These also indicate the mixture of morphological characters in this complex. The combination of multivariate analysis and RAPD data support the evidence for the complex.

Based on multivariate analysis, *E. racemosa* is more closely associated with *E. serratifolia* and differentiated from *E. giraldii*, suggesting that high elevation, dense shade limited of the migration of pollinators and fruit dispersal may restrict gene flow.

10. Revision of the genus *Exochorda*

Evidence from the present and earlier research can be used in an attempt to establish the relationship between *Exochorda* and other genera in Rosaceae.

Analysis of the relationship between *Exochorda* and other genera has been attempted by several authors. According to its wood anatomy, Zhang (1993) considered *Exochorda* to be more similar to the Prunoideae than to the Spiraeoideae, but the percentage of solitary vessels in the genus is larger than in the Prunoideae. Based on cytological evidence, Goldblatt (1976) suggested that *Exochorda* should be transferred to subfamily Prunoideae, this treatment "may be the most satisfactory way to reflect the natural relationship of the genus". The presence of arbutin and of a number of flavones in *Exochorda* leaves, links this genus chemically with certain Spiraeoideae (i.e. *Sorbaria*) or Maloideae (i.e. *Pyrus*) than with *Prunus* (Wallaart, 1980). Earlier on, Bonne (1928) realized that *Exochorda* was aberrant in Rosaceae. Stebbins (1958) also speculated that *Osmaronia* and *Exochorda* could be relicts of the prunoid ancestor of the Pomoideae. But morphologically, in leaf epidermis, *Osmaronia* shows more differences to *Exochorda* than similarities (Li Gang, 1993).

This genus does not fit conveniently in any of the four classical subfamilies and as such it undermines their status. A reappreciation of tribal subdivision in Rosaceae rather than subfamilial could refer *Exochorda* to its own tribe Exochordeae as is recognized today (Exochordeae) within Spiraeoideae.

10.1. Description of the genus

Exochorda Lindl. in Gard. Chron. 925. 1858; Benth. & Hook.f., Gen. Pl. 1: 612. 1865; Maxim. in Act. Hort. Petrop. 6: 230. 1879; Focke in Engler & Prantl, Nat. Pfl. fam. 3(3): 18. 1888; C.K. Schneid. Ill. Handb. Laubh. 1: 493. 1906; Nakai, Fl. Kor. 31: 473. 1911; Sarg. Pl. Wils. 3: 445. 1917; Diels, Syll. Pfl. 230. 1936; Rehder, Bibl. Trees & Shrubs 232. 1949; Boom, Ned. Dendr. 227. 1959; Hutch. Gen. Fl. Pl. 1: 179. 1964; Kom. Fl. U.S.S.R. 99: 244. 1971; Yu Te-Tsun, Fl. Sin. 36: 98, 1974.

Basionym: *Amelanchier racemosa* Lindl. Bot. Reg. 33. Pl. 38. 1847.

Homotypic synonyms: *Spiraea grandiflora* Hook.f. Bot. Mag., t. 4795, 1854; *Exochorda grandiflora* (Hook.f.) Lindl. in Gard. Chron. 925. 1858.

Type: ***Exochorda racemosa* (Lindl.) Rehder** China, near Ningbo, *R. Fortune 29*, 1846 (K).

Deciduous shrubs, 1-3 m high, young shoots erect, slender, cylindric, glabrous and reddish-brownish, old shoots brownish; buds triangular-ovate, apex obtuse, glabrous, purplish-reddish. Leaves elliptic, oblong-elliptic to oblong-obovate, 3-9 cm by 1.5-4 cm, entire, sparsely serrate above the middle, apex rounded-obtuse, acute or somewhat apiculate, base cuneate or broad-cuneate, glabrous on both surfaces; petioles 5-25 mm long; stipules caducous. Raceme 3-14 cm, flowers 3-12, glabrous, pedicels 3-8 mm, lower pedicels longer. The upper ones shorter, glabrous; bracts small, broad-lanceolate; flowers 25-45 mm in diameter; calyx tube shallow-campanulate, glabrous; sepals broad-deltoid, c. 2 mm long, apex acute or obtuse, serrulate at margin, glabrous, yellowish-greenish; petals 5, obovate, c. 20-28 mm by 5-19 mm, apex obtuse, base clawed, whitish; stamens 9-37, 2-7 inserted at the margin of the disk, opposite to the petals; carpels 5, connate; styles separate. Capsules turbinate, 9-13 mm by 9-13 mm, glabrous with 5 spines, purplish-brownish at maturity; seeds 8-10 mm by 4-6 mm, half-rounded, winged.

Distribution: From East Asia to Central Asia, native of China, N. Korea, S. Korea, Kirghizstan, Tadzhikistan, Turkestan and Uzbekistan. Cultivated as an ornamental spring-flowering shrub in gardens of the temperate zones. For vegetation ecological data in China see appendix I.

Vernacular names: China: Bai Juan Mei, Bai Shan Hua, Jin Gua Guo. English: Pearl bush.

10.2. Description of the species

Exochorda spp. have usually been described either from flowering or from fruiting specimens, without critical reference to type materials of earlier published species. The species names have been variously treated, and to date, no entirely satisfactory classification has been proposed for this genus.

The results obtained in the earlier chapters are used in this present revision to delimit taxa. Throughout the study, I developed a growing awareness that previous taxa in the genus *Exochorda* have more or less identical characters and variation is continuous over a large area of distribution. If we take into consideration the similar leaf epidermis, the uniform pollen morphology, the same wood type and numerical taxonomy, we have to conclude that all taxa are conspecific.

Table 10.1 shows that there are widely overlapping character states between different taxa as previously published. The differentiating characters are simply too weak for specific distinction, and mainly based on quantitative differences (Chapter 9) in which leaf shape and sizes show overlap. Consequently, all *Exochorda* species are reduced to a single one: *E. racemosa* (Lindl.) Rehder (description as for the genus) and only three subspecies can be maintained.

Table 10.1. Descriptive data for *Exochorda* species as extracted from the protologues

Names in previous classification	Stem & leaf	Flower & fruit
E. racemosa	Bark brown. Leaf 5-8 cm long, entire, petiole 1.3 cm long, apex acute & somewhat apiculate, glabrous	Flowers 6-8, stamens 15. Fruit not described
E. serratifolia	Stem unknown. Leaf 5.7 × 2.5 cm, petiole 1.3 cm, apex acute-serrate, base entire, pubescent, ovate or cuneate	Calyx lobes, rounded-ovate obscurely crenulate. Flowers subsessile, petals obcordate-spathulate, 1.6 cm long. Fruit unknown
E. korolkowii	Bark deep red-brown. Leaf petiolate, elliptic, narrow, entire or at apex irregularly serrate mucronate	Carpels compressed ellipsoid acuminate. Seed 1, compressed, winged, brown
E. giraldii	Stem unknown. Petiole 2.5 cm long, leaf entire, rarely indistinctly crenate-serrate	Fruit turbinate, 1.3 cm long
E. racemosa var. *wilsonii*	Branch pale brown to purple. Leaf 7 × 3.5 cm, obovate, ovate or elliptic dentate above the middle	Petals 2.5 cm long. Fruit turbinate, 1.5 cm long
E. serratifolia var. *oligantha*	Unknown	Flowers 1-2 per inflorescence
E. tianschanica	Leaf 2-3.5 (-4) × 1-1.8 cm, oblong, oblong-lanceolate, petiole 2-5 (7) mm long	Flowers 10-13 per inflorescence, inflorescence (7)8-10 cm long, stamens 25
E. serratifolia var. *polytricha*	Hairs on young branches. Hairy on lower surface and petiole	Hairs on axis of inflorescence and flower petiole

Key to the subspecies:

1. a. Leaves serrate above the middle, entire beneath the middle, elliptic or long-obovate. Stamens 13-29. First leaf of seedling obovate, fiddle-shaped. Distribution limited to Northeast China and the Korean peninsula..subsp. *serratifolia*

   b. Leaves entire, rarely serrate above the middle, ovate, long-ovate or long-obovate, and elliptic, oblong-elliptic to oblong-obovate. First leaf of seedling rounded to obovate or elliptic...2

2. a. Leaves ovate, long-ovate or long-obovate. Stamens 26-37. First leaf of seedling rounded to obovate, apex obtuse, margin rarely sparsely serrate above the middle. Distributed in Northwest and Central China ....subsp. *giraldii*

   b. Leaves elliptic, oblong-elliptic to oblong-obovate. First leaf of seedling elliptic, apex acute, margin serrate above 1/3 to 1/2 from the base. Distribution is disjunct in East China, Kirghizstan, Tadzhikistan, Turkestan and Uzbekistan ....subsp. *racemosa*

Figure 10.1. *E. racemosa* (Lindl.) Rehder subsp. *racemosa*, flowering habit: 1. Longitudinal section of a flower; 2. Floral diagram; 3. Longitudinal section of a locule, showing a seed; 4. Transverse section of a ovary, showing 5 carpels.

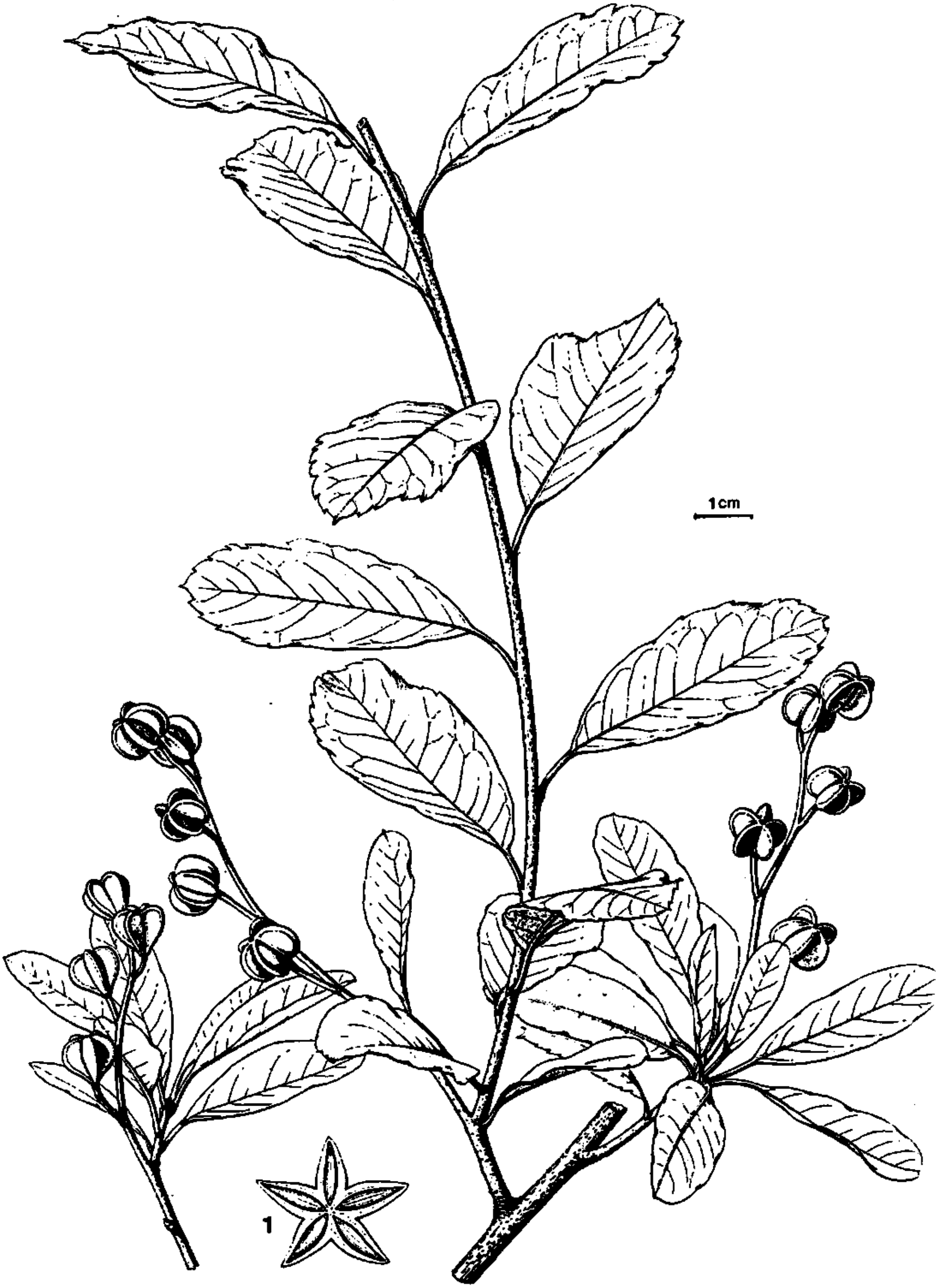

Figure 10.2. *E. racemosa* (Lindl.) Rehder subsp. *racemosa*, fruiting habit: 1. Transverse section of a fruit.

Original subspecies:

1. *Exochorda racemosa* (Lindl.) Rehder subsp. *racemosa*

***Exochorda racemosa* (Lindl.) Rehder** in Sarg. Pl. Wils. 1: 456. 1913 & in Jour. Arnold. Arb. 5: 174. 1924; Chengrong, Dendr. Sin. 492. 1937; Rehder, Bibl. Trees & Shrubs. 223. 1949; Boom, Ned. Dendr. 228. 1959; Yu Te-Tsun, Fl. Sin. 36: 99. 1974.

Basionym: *Amelanchier racemosa* Lindl. in Bot. Reg. 33. Pl. 38. 1847.

Type: China, Zhejiang prov., near Ningbo, *R. Fortune 29*, 1846 (K: holotype; LE, MO: isotype).

Homotypic synonyms: *Spiraea grandiflora* Hook.f. auct. non. Sweet 1870; Hook. in Curtis' Bot. Mag. t. 4795. 1854. ***E. grandiflora* Lindl.** in Gard. Chron. 925. 1858; Maxim. Act. Hort. Petrop. 6: 230. 1879; C.K. Schneid. Ill. Handb. Laubh. 1: 494. 1906.

Heterotypic synonyms: *Exochorda racemosa* var. *dentata* Rehder in Jour. Arnold. Arb. 7: 24. 1926. Type: Cultivated at the Arbold Arboretum under no. 7470 (plant received in 1913 from Léon Chenault & fils, Orleans, France).

***Exochorda korolkowii* Lavallée** (as Korolkowi), Icon. Arb. Segrez. 39. 1880; Rehder in Mitt. Deutsch. Dendr. Ges. 1914; Rehder, Bibl. Trees & Shrubs. 233. 1949; Krüssm., Handb. Laubh. 439-1960. **Type:** France, Chateau de Segrez, *Geo. Nicholson s.n.* 23-5-1885 K: lectotype, designated here. Paratypes: Segrez, Oct. 1884, *Nicholson s.n.* (K), Kew, May 9, 1895 *Nicholson s.n.* (K).

Cultivated from seeds sent by Korolkow, received by him from Nevessky who collected them in Bokhara, near Pombatschi and Karategin (1300-1500 m) late August 1878 (Gontscharov, 1934). The lectotype specimen is conserved at Kew (*Nicholson s.n.* 23-5-1885) and was collected in the Segrez Arboretum in France by Nicholson. Nicholson also collected a fruiting specimen in Oct. 1884 from Segrez and a flowering specimen from Kew on May 9, 1895, presumably from the same stock (*Lavallée 183.81*).

***Exochorda alberti* A. Regel** in Act. Hort. Petrop. 8: 696. 1884; C.K. Schneid. Ill. Handb. Laubh. 1: 493. 1906; Kom. Fl. U.S.S.R. 9: 244. 1971. ***Albertia simplicifolia* A. Regel,** Ind. Sem. Hort. Petr. 1883 nom.nud. ***E. grandiflora* var. *alberti* Asch. & Graebn.,** Syn. mitteleur. Fl. VI. 1900. **Type:** Turkestan, Tadzhik Mt.: Sorboch. Upper Amu Darya river in Karategin area 7-8000 feet between Tarif and Shingilifsh, *A. Regel s.n.* 18-30-Aug. 1881 (LE: holotype).

Heterotypic synonym: ***Exochorda tianschanica*** **Gontsch.** in Acta Univ. As. Med. Edi. Fasc. XXIII. Julio a. 1934. **Type:** Western Tian-schan, Jassy valley, Fergani Mt., *O. Knorring 646*, July 7, 1911, (holotype: LE; isotype: K, NY).

E. racemosa **f.** ***prostrata*** **(Schwer.) Rehder** in Cult. Trees & Shrubs. 232. 1949; ***E. grandiflora prostrata*** Schwer. in Mitt. Deutsch. Dendr. Ges. 16: 255. 1907; ***E. racemosa*** **var.** ***prostrata*** Rehder in Bailey Stand. Cycl. Hort. 2: 1194. 1914. **Type:** unknown.

This subspecies 1-4 m high. Leaves elliptic, oblong-elliptic to oblong-obovate, 3-6 cm by 1.5-4 cm, entire, sparsely serrate above the middle, apex rounded-obtuse, acute or somewhat apiculate, base cuneate or broad-cuneate, glabrous on both surfaces; petioles 5-15 mm long. Raceme 8-14 cm, flowers 5-12, glabrous, pedicels 3-8 mm, flowers 25-45 mm in diameter; calyx tube shallow-campanulate, glabrous; c. 2 mm long, apex acute or obtuse; petals 5, obovate, c. 23 mm by 18 mm, apex obtuse, base clawed; stamens 9-27, 2-6 inserted at the margin of the disk. Capsules 9-13 mm by 9-13 mm; seeds 8-10 mm by 4-6 mm.

Distribution: China: Anhui, Henang, Hubei, Jiangsu, Jiangxi, Zhejiang.
Kirghizstan: Kirgizia, Osh, Karategi, Vachshakii Mt.
Tadzhikistan: Bukhara, Khorog, Kulyab, Naudanak, Tavildara.
Turkestan: Kara-kirgizia, Ferganskii Mts.
Uzbekistan: Namangan.

Cultivated in Europe and America as an ornamental shrub.

Ecology: on wooded slopes, grassy hillsides, or rocky hills. Flowering from March to May; fruiting from August to October.

Altitude: 0-1500 m.

Vernacular names: China: Zhong Hua Bai Juan Mei, Jian Zi Hua, Jiu Huo Tou, Jin Gua Guo. English: Pearl bush.

Economic uses: *Exochorda* are cultivated as ornamentals.

Specimens examined (subsp. ***racemosa*****):**

China: Anhui province: Tianzhu Shan Mt.: *C. S. Fan & Y.Y. Li 73* (L). Yellow Mt.: *M. Chen 1103* (NF); *Li Gengyou et al. S 00432* (ZFC); *Wu Qiaoming 431052* (NF); *Wu Xiuliang s.n.* (NF). **Henang province:** Jiangjiawan: *Bai Cai s.n.* (BJFC). Lijiazhai: *Li Anren et al. 119* (PE). Xinyang: Jigong Shan Mt.: *Gao Fangyou 0068, 0069, 0070, 0071, 0073, 0074, 0075, 0076, 0105, 0107, 0108* (PE, WAG); *Guan Kejian 93229* (PE). Shangcheng: *HEAC expedition group, 1060* (HEAC). Xinxian: *HEAC expedition group 5305* (HEAC). **Hubei province:** Longchi Shan Mt.: Yixing: *Mao Shaohua et al. 191* (PE). **Jiangsu province:** Jiurong: Baohua Shan Mt.: *A.N. Steward 2135* (E, US); *E.D. Merrill 11488* (K, NY); *Guan Kejian 124* (PE); *Li*

Gengyou 130 (ZFC). Nanjing: Chadaokou: *Gao Fangyou 0052, 0053* (PE, WAG). Qixia Shan Mt.: *Gao Fangyou 0051* (PE, WAG). Mufu Shan Mt.: *M. Chen 206* (NF). Yuntai Shan Mt.: *Y.L. Keng 1636* (NY). Suzhou: Denwei Shan Mt.: *Gao Fangyou 0063, 0064, 0103* (PE, WAG); *Sun Sanshen et al. 13* (PE). Lingyang Shan Mt.: *Gao Fangyou 0056, 0057, 0062, 0091, 0092* (PE, WAG); *Liou Fangxun 875* (PE). Yi Xing: *Lin Gang 2383* (NF). Xiashu: *Gao Feng 043* (NF). **Zhejiang province:** Anji: *Zhang Cen 8* (NF). Hangzhou: Baishawan: *He Xianyu 0300* (NF). Beigaofeng Mt.: *Cheng Qichang 743* (HZU). Geling: *Gao Fangyou 0065, 0090* (PE, WAG). Jiulongtou: *Wu Changchun 35* (HZU). Mogan Shan Mt.: *Cheo & Wilson s.n.* (K, NY); *T.N. Liou 8092* (K). Tiantai: *HZU expedition group 28599* (HZU); *Zhou Huiyu 0440* (NF). Wuyun Shan Mt: *Cheng Qichang 566* (HZU). Zhuji: *M. Chen 875* (NF); *Veitch 198* (K). Pu Jiang: *Huang Zhigang S 2117* (ZFC); *Weng Yongfa S 5088* (NE); *Xiu Xinhua S 4108* (ZFC). Jiande: *Ding Chensen 770044* (ZFC). Ningbo: *E. Faber 1746* (K); *E.H. Wilson s.n.* (K); *C.W. Everard s.n.* (K). Shangyu: *expedition group 580* (ZFC). Zhuji: *Chen Hua J 8213-069* (ZFC); *Luo Jiangchen et al. J 8223-147* (ZFC); *Wang Meilong et al. J 8211075* (ZFC).

Kirghizstan: Arslanbob: *Abolin 674* (LE); *Lipsky 466* (LE); *O. Aqakhanyants & E. Chentsova 1120* (LE); *J. Bornmüller 893* (LE); *V.I. Botshanzev & T.V. Egorora 1472, 1529* (LE); *D. Divnogorskaya 492* (LE); *B. Fedtschenko s.n. 518, 854, 1449* (LE); *A.K. Golbek 217* (LE); *Gorbunov 1507* (LE); *Ilin 606* (LE); *R. Kamelin s.n.* (LE); *O.E. Knorring 145*; *Kornareva 1047, 4321* (LE); *S. Korshinsky 1125, 3047, 3049* (LE); *Lipsky 572, 573* (LE); *Litwinow s.n.* (LE); *Mussa s.n.* (LE); *Shidkova 345* (LE); *Yunusov 2, 2141* (LE). Fergan region: Andizhan distr. *Lipsky 4356* (LE); Arslanbob Mt.: *Lipsky s.n.* (LE). Jalalabad: Ferganskii Mt.: *A.A. Fedorov & E.M. Ilika 346* (LE); *S. Ikonnikov 11600* (LE). Osh: *N.N. Tuturin s.n.* (LE). Tshatkalskii Mt.: *Dzeus-Litowskaja 127* (LE).

Tadzhikistan: Khorog: *V.I. Botshantzev et al. 1529* (LE). Kulyab: *D. Divnogorskaya 492* (LE); *A. Pojarkova et al. 229, 473* (LE). Naudanak: *Kornareva 4321* (LE). Tavildara: *S. Korshinky 1125, 3049* (LE). Vakhsh river: *Yunusov 2141* (LE). Pamir: *Gorbunov 1507* (LE). South slopes of ridge Peter I, between villages Childors & Kha doza: *Shidkova 345* (LE).

Turkestan: Kara-Kirgizia: *P.S. Massaemov 418, 454* (LE). Kupai: *A. Regel s.n.* (K); Buchara: *A. Regel s.n.* (LE). Kuh-i-Frusch Mt.: *A. Regel s.n.* (LE).

Uzbekistan: Andizhan: *O.E. Knorring 1175* (LE); *Lipsky 4356* (LE); *Litwinow s.n.* (LE). Bukhara: *Fedtschenko 518, 854, 1449, 1543* (LE); *A.K. Golbeh 217* (LE); *Lipsky 572, 573* (LE); *Michelson 1* (LE); *S. Korshinsky 3047, 3048, 3050* (LE); Namangan: *B. Fedtschenko, s.n.* (LE). Lake Sary-chilak: *O.E. Knorring & T.G. Koko 426* (LE); *Rosheviz 282* (LE).

Notes: It is interesting to note that the distribution of this subspecies is disjunct. Separated by the Taklamakan and Gobi deserts, the two main regions inhabited are the new republics in Central Asia, and East China. The likely reasons will be discussed in Chapter 11. Figure 10.3 shows the variation of leaf shape, size and the serration of the leaf margin within one population (subsp. *racemosa*: Pop. 10; subsp. *giraldii*, Pop.16; subsp. *serratifolia*, Pop. 19). Serrate leaf margins are not restricted to subspecies *serratifolia*, and serration may vary within a specimen.

Orthographic variants of korolkowii, the second declension of korolkowius, a latinization of Korolkow are frequently used: korolkovii following another transcription of the Russian W (B), and korolkowi, the second declension of Korolkowus, another latinization of Korolkow (see also Backer, 1936: 307).

Hybrid cultivar:

***Exochorda racemosa* 'The Bride'** in Ill. Handb. Laubh. 1: 493. 1906; C.K. Schneid. Ill. Handb. Laubh. 1912; Rehder, Bibl. Trees & Shrubs. 232. 1949; Boom, Ned. Dend. 228. 1959; Krüssm., Handb. Laubh. 1: 438. 1960----*Exochorda alberti macrantha* Lemoine, Gat. 152: vii. 1902.

Originally published as *E. macrantha* (Lemoine) C.K. Schneid. 'The Bride'. A hybrid raised about 1900 by Messrs Lemoine of Nancy, France, from "*E. korolkowii*" fertilized with pollen of "*E. racemosa.*".

In *Exochorda, E. racemosa* 'The Bride' is the only known genotype with pendulous branches. Further characters are as in *E. racemosa* (Lindl.) Rehder subsp. *racemosa.*

Cultivated in Europe.

Vernacular names: English: Irish Pearl.

Another cultivar (not seen) is 'Irish Pearl' (= 'The Pearl'), also of hybrid garden origin with vigorous growth, flowering shoots very long, to 90 cm (Huxley, 1992).

2. *Exochorda racemosa* (Lindl.) Rehder subsp. *giraldii* (Hesse) F.Y. Gao & Maesen stat. nov.

Type: China, South Shaanxi. *J. Giraldi s.n.* 1897 (K).

Basionym: *Exochorda giraldii* Hesse, Schwer. Mitt. Deutsch. Dendr. Ges. 17: 191. 219. 1908; Bean, Trees & Shrubs Brit. Isl. 1: 548. 1919; Chenrong, Sin. Dendr. 493. 1937; Rehder, Bibl. Trees & Shrubs. 233. 1949; Boom, Ned. Dendr. 28. 1959; Krüssm. Handb. Laubg. 1: 438. 1960; Yu Te-Tsun, Fl. Sin. 36: 98. 1974; ***E. racemosa* (Lindl.) Rehder var. *giraldii* (Hesse) Rehder** in Sarg. Pl. Wils. 1: 457. 1913.

Heterotypic synonyms: *Exochorda racemosa* (Lindl.) Rehder var. *wilsonii* Rehder in Sarg. Pl. Wils. 1: 456. 1913. **Type:** China, Western Hubei (Western Hupeh), *E.H. Wilson 397*, May 1907 & Oct. 1907, (holo: K; iso: E, US).

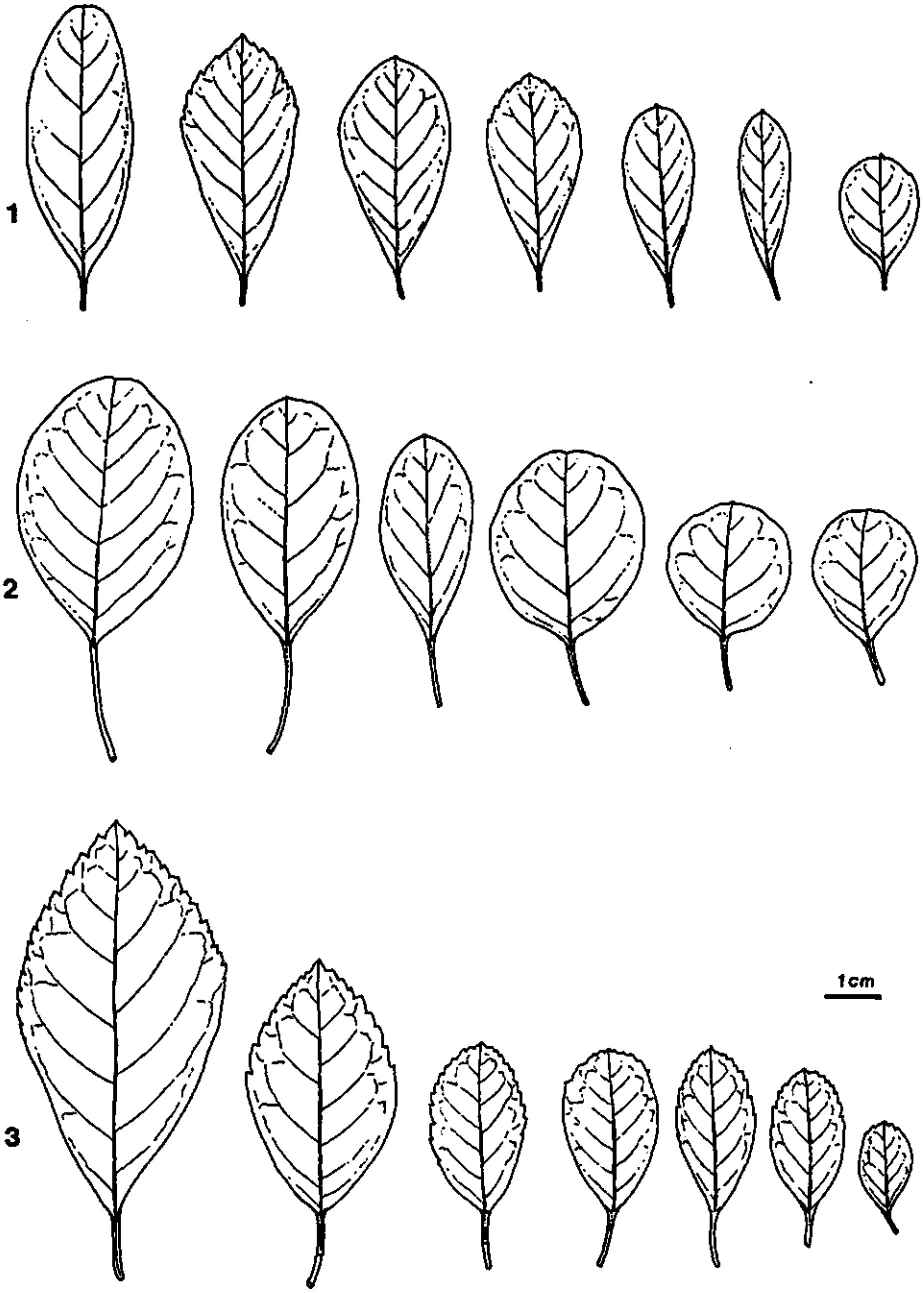

Figure 10.3. The variation of leaf shape, size and the serration of the leaf margin.
1. *E. racemosa* subsp. *racemosa* (Pop. 10); 2. *E. racemosa* subsp. *giraldii* (Pop. 16); 3. *E. racemosa* subsp. *serratifolia* (Pop. 19).

***Exochorda giraldii* Hesse var. *tomentosa* Wuzhi** in Fl. Hupehensis, 2:122. 1979. **Type:** (not seen).

The subspecies *giraldii*, differing from the subsp. *racemosa*, is 1.5-4 m high. Leaves ovate, long-ovate or long-obovate, 3-4 cm by 1.5-3 cm, apex rounded, obtuse and apiculate, base wide-cuneate, entire, sparsely serrate above the middle, glabrous; petioles slender, base reddish, glabrous, 15-25 mm. Raceme 5.5-11 cm, flowers 5-12, 30-45 mm in diameter, pedicels c. 1 mm; petals 20-28 mm by 9-17 mm; stamens 26-37. Capsules 10-12 mm by 10-12 mm, seeds 8-10 mm by 4-6 mm.

The subspecies was introduced to Europe by seeds sent by Giraldi. Mr. Hermann Hesse, of Weener, in N.W. Hanover (Germany) first cultivated it in his nursery and described it as a new species of shrub.

Distribution: endemic to China: Gansu, Shaanxi, Shanxi,

Ecology: on slopes, at riversides, on high hills. Flowering from April to May; fruiting from August to October.

Altitude: 1000-2000 m.

Vernacular names: China: Ji Shi Bai Juan Mei, Red petiole Bai Juan Mei. English: Wilson pearl bush.

Specimens examined (subsp. *giraldii*):

China: Gansu (Kansu) province: Cheng Xian: *Wei Zhiping 2266* (WG). Hui Xian: *Wei Zhiping 069* (WUG). Tianshui: *W.Y. Hisa 5621* (PE). Zhouqiu: *Guo Benzhao 5578* (WG). S.W. Gansu: *J.F. Rock 14739* (E, LE), *15059* (K). S. Gansu: *R. Farrer et al. 6* (E, MO); *R. Farrer & W. Purdom 95* (E, KYO). **Shaanxi province:** Chunhua: Hu Xian: *Li Peiyuan 10105* (WG); *Fu Kunjun 14534* (WG); *Yang Maoshen 059* (WH). Hua Shan Mt.: *Gao Fangyou 0080* (PE, WAG); *Huo Shuhua 56-3331* (BJFC); *Wang Hongjie 17* (WG, WH); *Wang Zuobin 17814* (WG), *19643* (PE, WG); *Zhang Zhiying 18394* (WG). Luoyang: *Wang Zuobin 18715* (WG, WH). Mei Xian: *Wang Zuobin 13765, 17714* (WG). Shanyang: *Zhang Zhiying 15870* (WG); Taibai Shan Mt.: *K.T. Fu 2546* (PE); *Gao Fangyou 0077, 0078, 0079, 0109, 0110, 0111, 0112, 0113* (PE, WAG); *W. Purdom 1* (K); *Wei Zhiping et al. 1278* (WG). **Shanxi province:** Gangcheng: *Bao Shiying 550* (PE). Lingkong Shan Mt.: *Guan Kejian 484, 713* (PE). Lingshi: Shigao Shan Mt.: *Gao Fangyou 0081, 0082, 0114, 0115* (PE, WAG); *Huo Shuhua 0061* (BJFC, PE, WA). Yongji: *Liu Tianwei 0049* (PE). Zhongtiao Shan Mt.: *Huo Shuhua 56-3174* (BJFC).

Cultivated: **The Netherlands:** WAU: *J.v. Veldhuizen 1435, 1441* (WAG).

Notes: The distribution of this subspecies in between the disjunct distribution of subsp. *racemosa* should be noted in relation to its more montane character, i.e. altitudes above 1000 m.

Certain environments can give rise to extreme ecophenes in a wide range of species. For example, because of poor, dry soil conditions, population 18 from Shigao Shan Mt. (Shanxi prov., China) is dwarf (1.5 m) and populations 15, 16, 17 (from more fertile soils in Shaanxi prov.) are tall (up to 3-4 m).

3. *Exochorda racemosa* (Lindl.) Rehder subsp. *serratifolia* (S. Moore) F.Y. Gao & Maesen comb. et stat. nov.

Basionym: ***Exochorda serratifolia*** **S. Moore** in Hook. Ic. Pl. Ser. 3. Deel 3. p. 44. t. 1255 1877; Maxim. in Act. Hort. Petrop. 6: 231. 1879; C.K. Schneid. Ill. Handb. Laubh. 1: 494. 1906; Nakai, Fl. Kor. 31: 473. 1911; C.K. Schneid. Ill. Handb. Laubh. 46. 1912; Chenrong, Dendr. Sin. 493. 1937; Rehder, Bibl. Trees & Shrubs. 232. 1949; Boom, Ned. Dendr. 228. 1959; Tu Te-Tsun, Fl. Sin. 36: 100. 1974.

Type: China, Liaoning province, Qianshan (Chienshan) Mt., *John Ross 310*, May 11, 1876 (K).

Homotypic synonym: ***Exochorda serratifolia*** **S. Moore var. *typica* Nakai** in Bot. Mag. Tokyo 469. 1928.

Heterotypic synonyms: ***Exochorda serratifolia*** **S. Moore var. *oligantha* Nakai** in Bot. Mag. Tokyo 469. 1928. **Type:** Korea, Zuiko, Kokai prov., *Nakai 2439* (TI).

Exochorda serratifolia **S. Moore var. *polytricha* C.S. Zhu,** Acta Phytotax. Sin., 32(5): 432, 1994. **Type:** China, Henan province, Tiantan Shan Mt., *H.M. Shi s.n.* (HEAC) (not seen).

This subspecies, differing from the sub. *racemosa*, is 1-2 m high, leaves elliptic or long-obovate, 5-9 cm by 2-4 cm, apex acute or rounded-obtuse, base cuneate or broad-cuneate, serrate above the middle, entire beneath the middle, young leaves somewhat pilose on lower surface, old leaves glabrous on both surfaces, pinnate, lateral nerves somewhat curved; petioles 10-20 mm, glabrous, estipulate. Raceme 3.5-8.5 cm, flowers 3-7, glabrous, pedicels 2-3 mm long; flowers 30-40 mm in diameter; calyx tube shallow-campanulate, glabrous; petals 10-19 mm by 5-10 mm; stamens 13-29. Capsules 8-10 by 10-13 mm; seeds 6-10 mm by 5-6 mm.

Distribution: Northeast China: Liaoning, Hebei. **N. Korea & S. Korea.**

Ecology: on hill slopes and sandy soils. Flowering from April to May; fruiting from July to October.

Altitude: 250-800 m.

Vernacular names: China: Chi Ye Bai Juan Mei, Yu Ye Bai Juan Mei.

Notes: The origin of the type is uncertain. On the type specimen the locality was given as W. of Hingjing, Prov. Shing King, N. China. In the protologue the locality was described as Qianshan Mt., Liaoning province, China.

Probably *E. serratifolia* S. Moore var. *polytricha* C.S. Zhu should be *E. racemosa* var. *polytricha*. From the description it is not clear, and the type mentioned could not be inspected. This variety is said to differ by its hairs on young branches, lower surface, petiole, axis of inflorescence and flower petiole, but these characters fall within the range of the subsp. *racemosa*.

Specimens examined (subsp. *serratifolia*):

China: Hebei province: Wuling Shan Mt.: *Gao Fangyou 0083, 0084, 0089* (PE, WAG). **Liaoning province:** Beizhen: *Li Jiyun et al. 682* (IFP); *Li Jiyun 706* (IFP). Chaoyang: Fenghuang Shan Mt.: *Deng Yucheng et al. 717* (IFP); *Fu Peiyun 252* (IFP); *Gao Fangyou 0085, 0116, 0117, 0118* (PE, WAG). Fuxin: Haitang Shan Mt.: *Gao Fangyou 0086, 0087, 0088, 0119, 0120, 0121* (PE, WAG). Jianpin: *Wang Chongshu et al. 2982, 3512* (PE). Kezuo: *Wang Chongsu 3710* (IFP). Lingyuan: *Cui Shunchang 602* (IFP); *Li Shuxin 204* (PE). Xiongyue: *Gu Cuizhi 41* (PE).

N. Korea: Chyöng-jin: Ham-gyöng: *T. Nakai s.n.* (TI); Kaugkai: *R.G. Mills 56* (K). N. Heian: *E.H. Wilson 10576* (K). Yong Weol: *Wakehurst 260* (K).

S. Korea: Kyong-geui: circa Seoul: *S. Sugiyama* (see Nakai: Flora Koreana, 1911).

11. Geographical distribution of *Exochorda* and evolutionary trends

11.1. Introduction

Geographical differentiation exists between taxa at all levels and in all degrees of spatial separation, because different taxa may possess different powers of migration. Each taxon exhibits a pattern of distribution, which also is one aspect of its definition. The coincidence or not of areas occupied by related taxa has a bearing on the classification within the group, especially when the evolution of the group is taken into consideration (Stace, 1989).

Wild *Exochorda* only occurs in East and Central Asia of the Northern temperate zone. They are found on hills, slopes and valleys or forest edges. The station may be exposed and dry, or densely vegetated and humid. In exposed and dry environments, plants tend to be short and small. In closed moist vegetations, plants tend to be larger and more vigorous. Populations can be found on sandy soil or brown earth. The requirements for cultivation are apparently not very demanding, but calcareous soils are less suitable (Huxley, 1992).

11.2. Present geographical distribution of the genus

The genus *Exochorda* occurs in China, N. Korea, S. Korea and Kirghizstan, Tadzhikistan, Turkestan and Uzbekistan. Some subspecies are also cultivated in Europe and north America. The southernmost occurrence of *Exochorda* is represented by *E. racemosa* subsp. *racemosa* at 29°15' N, 121°05' E on Tiantai Shan Mt., Zhejiang province in East China (Zhou Huiyu 0440, NJFU); the easternmost by *E. racemosa* subsp. *serratifolia* at 128°27' E, 37°12' N in Korea (Wakehurst 260, K); the northernmost and westernmost by *E. racemosa* subsp. *racemosa* at 40°00'N, 72°30' E in Fergana Mt., Kirghizstan (Pryazin s.n., K). The species grows at altitudes between 0-2600 m, the highest altitude 2600 m is occupied by *E. racemosa* subsp. *giraldii* in Taibai Shan Mt., Shaanxi province of China (Wei Zhibin et al. 1278, WUG). There are no distribution details for Europe and America, where the shrub is planted in gardens.

E. racemosa subsp. *giraldii*, is endemic in Northwest and Central China. Shanxi prov.: Huo Xian, Lingshi, Yongji; Shaanxi prov.: Hua Shan Mt., Taibai Shan Mt., Chunhua, Hu Xian, Mei Xian, Shanyang, Zhouzhi; Gansu prov.: Hui Xian, Cheng Xian, Tianshui, Zhouqiu (Table11.1).

E. racemosa subsp. *racemosa*, occurs in East China. Jiangsu prov.: Nangjing: Qixia Shan Mt.; Suzhou: Lingyan Shan Mt., Dengwei Shan Mt.; Jiurong: Baohua Shan Mt.; Zhejiang prov.: Hangzhou: Mogan Shan Mt., Ningbo, Pujiang, Tiantai Shan Mt.;

Zhuji; Henan prov.: Shangcheng, Xin Xian, Xinyang: Jigong Shan Mt.; Anhui prov.: Huang Shan Mt.; Hubei prov.: Jianshi. Turkestan. Kirghizstan: Fergana Mt.

E. racemosa subsp. *serratifolia* occurs in Northeast China and the Korean peninsula. Hebei prov.: Xinglong: Wuling Shan Mt.; Jilin prov.: Changbai Shan Mt.; Liaoning prov.: Beizhen, Kezuo, Lingyuan, Jianping, Chaoyang: Fenghuang Shan Mt.; Fuxin: Haitang Shan Mt.; D. P. R. Korea: Yong Weol, Heian; P. R. Korea. Table 11.1 and Fig. 11.1 show the present geographical distribution of the genus.

As shown in Table 11. 1 and Fig. 11.1, the distribution areas of different subspecies or populations of *Exochorda* are quite disjunct. A boundary of distribution can be recognized for these subspecies, extending northwest from China to Kirghizstan, Turkestan and Uzbekistan through Central China, Northwest China, and it extends northwards to the Korean peninsula, where it appears to be represented by *E. racemosa* subsp. *serratifolia*, the same subspecies as that in adjacent Northeast China. The probable reason for the distribution will be discussed in the following paragraph.

Table 11.1. The distribution of *Exochorda racemosa* in China and adjacent areas

Subspecies	JL	LN	HEB	JS	AH	ZJ	HN	HUB	SX	SHX	GS	SK	NK	K	Ta	T	U
subsp. *giraldii*									+	+	+						
subsp. *racemosa*				+	+	+	+	+						+	+	+	+
subsp. *serratifolia*	+	+	+									+	+				

1: Provincial names are arranged from the north to the south, and the east to the west, according to the Atlas of P. R. China (1989).

2: JL-Jilin prov.; LN-Liaoning prov.; HEB-Hebei prov.; JS-Jiangsu prov.; AH-Anhui prov.; ZJ-Zhejiang prov.; HN-Henan prov.; HUB-Hubei prov.; SX-Shanxi prov.; SHX-Shaanxi prov.; GS-Gansu prov.; SK-D. P. R. Korea; NK-R. O. Korea; K-Kirghizstan; Ta-Tadzhikistan; T-Turkestan; U-Uzbekistan.

11.2.1. The types of distribution

According to Takhtajan's floristic regions of the world (1986), *Exochorda* belongs to the Eastern Asiatic and Irano-Turanian regions. Table 11.1 and Fig. 11.1 show that *Exochorda* has a concentrated distribution in the East Asian region. On the basis of Wu Zhengyi's floristic division for China (1979), *Exochorda* belongs to the Sino-Japan Forest Subkingdom. Table 11.2 shows the areas of distribution of the *Exochorda* complex following the floristic classifications of Takhtajan (1986) and Wu (1979).

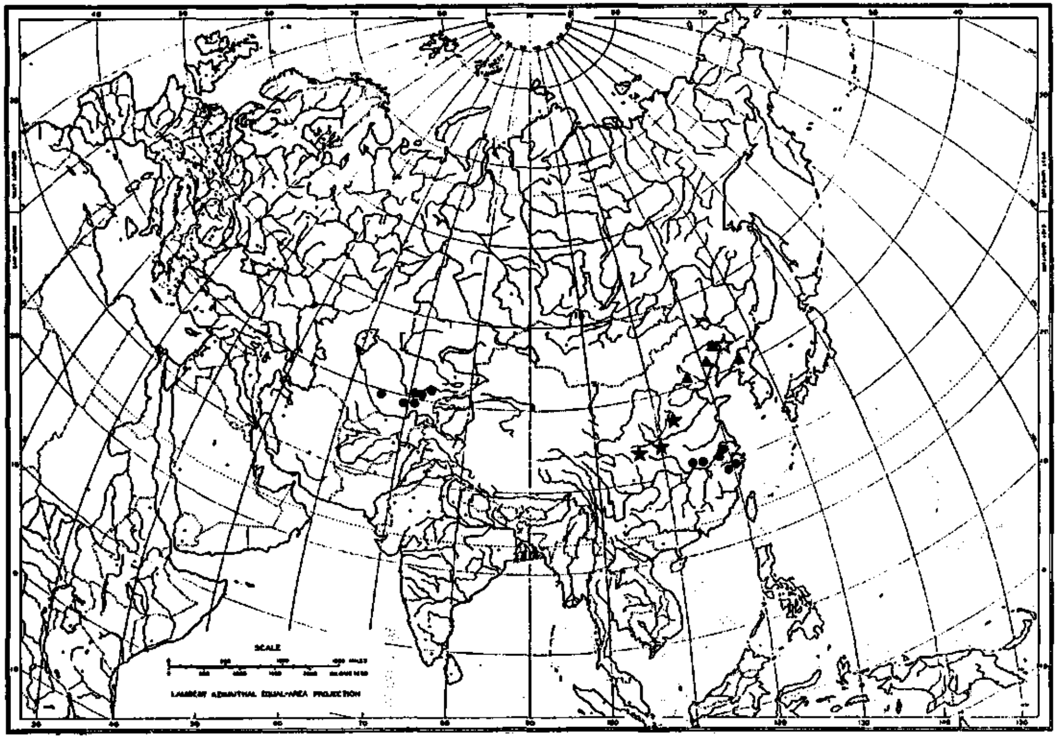

Figure 11.1. Distribution of *Exochorda*. ●: *E. racemosa* subsp. *racemosa*;
★: *E. racemosa* subsp. *giraldii*; ▲: *E. racemosa* subsp. *serratifolia*.
☆: fossil distribution.

Table 11.2. The distribution of *Exochorda* in the floristic regions of the world

Subspecies	Eastern Asiatic Region	Irano-Turanian Region	Sino-Japan Forest Subkingdom
subsp. *giraldii*	+		+
subsp. *racemosa*	+	+	+
subsp. *serratifolia*	+		+

11.2.2. Centre of diversity

A centre of genetic diversity is such an area where there are one or more areas with a marked concentration of species. Zeven and Zhukovsky (1975) defined twelve such centres for important crop plants. When the centres of genetic diversity for non-crop species are similarly plotted, they are mostly found to coincide with those of the crop species (Stace, 1989). Among these twelve centres, East China is one of the three major centres. Vavilov (1951) believed that the centres of diversity were also the centres of origin of the taxa concerned.

The centre of a floristic region is determined by the following two principles: 1. A large number of species is concentrated in a certain district, namely the center of the majority; 2. Species of a district can reflect the main stages of the systematic evolution of the plants, namely the centre of diversity (Lu Anmin, 1982). The centre of the present distribution does not imply the place of origin and differentiation centre. The place of origin of a taxon may be: 1. The place where the earliest fossils were found; 2. The place where primitive species are concentrated and different differentiation periods are included; 3. No tremendous changes have taken place after species development.

From the Table 11.1, Table 11.2 and Fig. 11.1, it can be inferred that the Sino-Japan Forest Subkingdom is the place where all subspecies are formed and most available diversity occurs. In the East Asian region, there are three subspecies in the north temperate zone between 29°00' N to 42°00' N, 105°00' E to 128°00' E. This region is now the centre of diversity and geographical distribution of *Exochorda*.

11.3. Time and place of origin

The origin of *Exochorda* can not be demonstrated palaeontologically, and must be the subject of conjectural and speculative hypotheses. The time, place, ancient flora and dispersal route can be inferred from some facts. Fossil records play an important role in the discussion of origin and dispersal of taxa.

The development of adaptation radiation in Angiosperms has been closely related to the paleoclimate and paleoenvironment. Several environmental factors, influencing each other, have affected the evolution or development of the Angiosperms, which can be divided into different stages. The boundaries between these stages are not can be divided into different stages. The boundaries between these stages are not consistent with the traditional geological ages, therefore, floristic regionalization might better be based on the stages of development.

Based on evidence from O_2 isotope determination, the Cretaceous era (135-60 million years ago) has been established during the warmest period in the history of the vegetated earth. The temperature from the equator to polar regions was higher than at present. The regions with a climate similar to our present tropical-subtropical conditions might have extended to 45° N and 70° N (Tao Junrong, 1992). In the late Cretaceous, China was mainly situated in the tropical and subtropical zone (5° - 40° N). Northeast China had a subtropical or warm temperate climate (Tao Junrong, 1992), and other regions including southeast China were dry (Sun Xianjun, 1979). Palaeogeographical material has shown that the continental shelf of the Bohai Sea and the Yellow Sea of China were contiguous to the continent in the Late Cretaceous and Palaeocene. Because of the movement of the Pacific and the India tectonic plates, China moved north 10° - 13° during the Late Cretaceous to the Quaternary. The changes in position and sea level, and the mountain uplift led to a climate cooler than before (Hsu Ren, 1983). During the Eocene (54-38 million years ago), North China had a subtropical climate, and the flora consisted mainly of deciduous broad-leaved forest and evergreen broad-leaved forest. By the Late Tertiary, the average yearly temperature had dropped 1° - 10° C, the climate of north China became cooler and drier (Tao Junrong, 1992). During the Quaternary stage, the mountain glaciers in China were influenced by global glacial-interglacial alternations due to the climatic fluctuation. These climate fluctuations apparently affected the distribution of plants. The components of the flora were different or slightly similar from those of the present (Tao Junrong, 1992).

About the origin of *Exochorda*, the principal barrier is the extreme poverty of the fossil records, only one fossil specimen was found in Fushun (41°51' N, 123°55' E), Liaoning province of China (Fig. 11.1) from Eocene onwards (Plant Fossils of China, Vol. III, 1978; Li Xingxue, 1995). The fossil species was named *E. antiqua* Li, and it is similar to the single existing species. Although it is very difficult to postulate the initial place of origin, it gives a chance to trace the origin and development in the past. Figure 11.1 shows the fossil distribution and present geographical distribution of *Exochorda*. Table 11.3 shows fossil records of some genera of Rosaceae and their distribution. After *Sorbaria* and *Spiraea*, *Exochorda* is apparently one of the earlier Rosaceae detected as fossil.

In the Eocene, at the time of the climate optimum, the north-Tethyan floristic belt reached the zenith of its development both in terms of spatial extension and floristic diversity (Kubitzki, 1996). The flora in Fushun (Northeast China) during the Eocene was represented by evergreen and deciduous forest that grew in a subtropical climate, subject to warm and humid conditions, summer flooding and winter droughts. Similar flora was also found in northeast China, for example, in the Heilongjiang province: Yanshou, Yilan; Jilin province: Hailong, Huichun; Liaoning province: north Shenyan;

Shandong province: Pingdu (Li Xingxue, 1995). At present the aforementioned regions belong to temperate zones with a short summer and long winter, and spring droughts, summer flooding and autumn frost.

One attempt has been made (Lu Lingti, 1996) to analyze the origin of the genus *Exochorda*. On the basis of fossil records (Plant Fossils of China, 1978), it was deduced that the genus *Exochorda* probably originated in the temperate mountains of East Asia, no later than the Eocene, probably already in the Early Tertiary or Palaeocene. At the present state of knowledge, it cannot be ascertained exactly where was the origin for this genus. Since its origin, this region has been sliced up so much by the formation of the Taklamakan and Gobi deserts that it may be impossible to ever resolve this problem.

11.4. Dispersal and evolutionary trends

The correlation between geographic distribution and phenotypes of the complex raises interesting questions regarding population dispersal and biogeography.

The ultimate collision of the India Plate with the Eurasian Plate in the Miocene led to punctuated uplift and the step-wise development of the monsoonal climate. The uplift of the Qinghai-Tibetan Plateau instigated further changes to the monsoonal climate (Ferguson, 1993). During the Pleistocene temperature changes alternately strengthened the summer and winter monsoons, in such a way that a warm humid phase was followed by a cold dry phase. Central Asia dried up as the roughly east-west oriented mountain chains rose. At this stage colonization was only possible from east to west or from west to east along the vast corridor linking the European Alps to the Qinling Mountains, the interchange was possible along this thoroughfare and depended on the dispersal potential of the species (Ferguson, 1993).

By the Late Pleistocene, the east-west running Qinling Mountains effectively blocked the retreat of the thermophilous organisms in the glacial phases. And it provided the "shelter" during glacial periods, so many plants which had a widespread distribution in the Northern Hemisphere in the course of the Tertiary have also been able to survive during the Quaternary. At the present day, the Qinling Mountains form one of the most important biogeographical boundaries in China. It also formed a barrier to *Exochorda* dispersal (see Fig. 11.1). This seems to offer the best explanation for the absence of *Exochorda* from the southern slope of Qinling. The only escape route left was via the Chang Jiang River (Yangtze River) plains and the low hills near Nanjing. This can be certified by the low latitudes in Chang Jiang River plains where individuals of *Exochorda* are commonly found. At other times the only way into Northeast China was via the low hills and plains to the north and east. This explains the migration of *Exochorda* to East China and Northeast China.

Table 11.3. Fossil records of some genera of Rosaceae and their distribution

Genera	Cretaceous			Palaeocene		Eocene			Oligocene		Miocene			Pliocene		Locality	Literature
	L	M	U	L	U	L	M	U	L	U	L	M	U	L	U		
Amelanchier												__a			__b	a: Neimongol, China	Li, 1995
																b: Taigu, China	Li, 1995
Cotoneaster												—					Tao, 1992
Crataegus												—		—	—	Shaanxi, Tibet, China	Li & Tao
Exochorda							—									Fushun, China	PFC, 1978
Malus												—					
Physocarpus										__a		__b			__c	a: Hazakhstan	Takhtajan, 1963
																b: Linqu, China	PFC, 1978
																c: Germany	Takhtajan, 1963
Prunus												—					
Rosa							—					—				Fushun, China	Li, 1995
Sorbaria	__a											__b				a: Wuyun, China	Tao, 1992
																b: Kazakhstan	Takhtajan, 1963
Sorbus												—					
Spiraea					__a	______	______	______a		__b		__c		__d		a: Alaska, U. S. A.	Takhtajan, 1963
																b: Kazakhstan, Siberia & Europe	PFC, 1978
																c: Linqu, Shandong, China	PFC, 1978
																d: Tarim Pendi, Xinjiang, China	PFC, 1978
Stephanandra							—	—								Altay & Ural	Takhtajan, 1963

L: Lower; M: Middle; U: Upper.

Li, 1995: quoted from Li Xingxue, 1995.

Tao, 1992: quoted from Tao Junrong, 1992.

Takhtajan, 1963: quoted from Takhtajan et al., 1963.

PFC: Plant Fossils of China, 1978.

The species may have originated and developed after Laurasia was broken up. With the plate movements, they moved from the centre of origin to the northeast (Korea); to the northwest (Tian Shan Mt.) and to central Asia along the Loess Plateau. Subsequently they developed or changed in different regions with the changes of the paleoclimate and paleogeography and formed the present distribution pattern.

This raises the question as to how a species manages to acquire such a vast geographic range.

Seeds dispersal by water may be a cause, as seeds of *Exochorda* are lighter than water, and may float more than 24 hours in water without loosing germination capacity (Chapter 5). Seed dispersal by wind and gravity is also a consideration. When the fruit capsule bursts, seeds can be ejected. This is effective for a species to colonize a new locality over considerable distance. Moreover, wild seeds transported by man is a possibility, and will promote gene flow. The dry capsule is hardly attractive to birds. Dispersal by root suckers is another possibility. I observed new branches sprouting from roots when I did field work in China in 1995.

The comprehensive study showed differences between three groups, however, these differences were not very substantial. This suggests that these taxa share a common ancestor and may be of relatively recent origin. Probably the ancestral diploid species must have adapted to both drier continental and moist coastal environments. Figure 11.2 shows putative relationships and evolutionary trends in the complex.

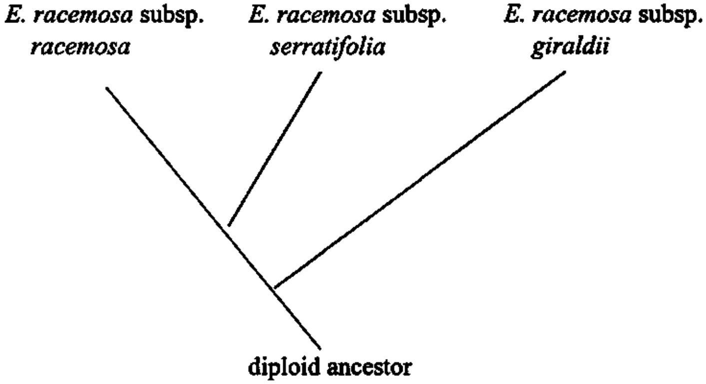

Figure 11.2. Putative phylogenetic relationships in the *Exochorda* complex.

11. 5. Discussion and conclusions

From the fossil records and geographical distribution of *Exochorda* it can be concluded that *Exochorda* has a relatively narrow and disjunct distribution limited to East Asia and Central Asia where conditions are similar to the area where fossils have been found. Based on the species analysis, East Asia (mainly China) is the centre of geographical distribution and diversity.

It is inferred that *Exochorda* originated in the temperate mountain zone of East Asia, East China and Northeast China. The earliest leaf fossil was found in Fushun, Liaoning province, northeast China before the Eocene. The time of origination dates back to the Early Tertiary or Palaeocene.

The formation of the present distribution pattern shows that different subspecies have their concentrated distribution, i.e. the distribution of different subspecies is either contiguous or disjunct. The explanation for this disjunction can be sought in the continuing uplift of the Himalaya and the Qinghai-Tibetan Plateau. Northwest China has been largely drought-prone since the Oligocene (Ferguson, 1993).

The Taklamakan Desert (Taklamakan Shamo) originated in the Quaternary Period and developed rapidly in the second half of the Tertiary Period (c. 40 million years ago) after the uplift of the Himalaya, collision of the India Plate with Eurasia and disappearance of the Old Mediterranean in the Oligocene, namely after the Eocene (Wu Zhenyi et al., 1983). It can be logically deduced that *Exochorda* originated before the emergence of the Taklamakan Desert. The genus probably once occupied a large area in the northern hemisphere of Asia. The formation of the present distribution pattern and reasons for this formation might be deduced as follows: dry climate in a large portion of the Taklamakan Desert and adjacent areas; different edaphic conditions and precipitation; and the continental drift. A formerly continuously distributed taxon became separated into different areas and has been subjected to divergent evolution there. The disjunct pattern may represent the relict of former wide, continuous distribution patterns, the intervening areas having been depopulated by the rigours of the climate.

Different habitats may bring about different selective forces and lead to morphological differences and developmental characters and to the establishment of populations. The equation Genotype + Environment → Phenotype implies that the phenotype is not merely a manifestation of the genotype, but that environment factors play a part in modifying the genotype to produce various phenotypes (Stace, 1989). Certain environments can give rise to extreme ecophenes in a wide range of species. For example, population 06 (Dengwei Shan Mt., Suzhou, China) is distributed along a plantation, the dynamics of this habitat will cause the population to diminish or become extinct. On the other side, under favourable conditions, such as in a national park, populations 15, 16, & 17 may quickly colonize new sites.

With the increase of population and the reduction of forest areas, I found some plants of *Exochorda* only in forest reserves or on hill tops. The type specimen of *Exochorda racemosa* (Lindl.) Rehder was collected by R. Fortune in 1846 (Fortune 29, K) "in the mountains near Ningbo, Zhejiang province, China", but I did not find specimens in Ningbo when I worked in the fields nor specimens from Ningbo in the herbarium. The type specimen of *Exochorda serratifolia* S. Moore was collected by J. Ross in 1876 in North China (J. Ross 310, K). Collection records did not show the exact location although some publications have quoted Qian Shan Mountain, Liaoning province, China. I did not find specimens in Qian Shan Mountain and in the herbaria either. Names of locations may have changed, so tracing specimens is difficult. Anyway, it is likely that a century ago the distribution of *Exochorda* genotypes has been wider than today.

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- **DBN:** Herbarium, National Botanical Gardens, Glasnevin, Dublin, Ireland.
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- **HZU:** Herbarium, Biology Department, Hangzhou University, Hangzhou, Zhejiang, China.
- **IFP:** Herbarium, Institute of Applied Ecology, Academia Sinica, Shenyang, Liaoning, China.
- **K:** Herbarium, Royal Botanical Garden, Kew, England.
- **KYO:** Herbarium, Botany Department, Kyoto University, Japan.
- **L:** Rijksherbarium, Leiden, the Netherlands.
- **LE:** Herbarium, V.L. Komarov Botanical Institute of the Academy of Sciences of the U.S.S.R. Leningrad, U.S.S.R.
- **MO:** Herbarium, Missouri Botanical Garden, Missouri, U.S.A.
- **NEFI:** Herbarium, Northeast Forestry University, Harbin, Heilongjiang, China.
- **NF:** Dendrological Herbarium, Forestry Department, Nanjing Forestry University, Nanjing, China.
- **PE:** Herbarium, Institute of Botany, Chinese Academy of Sciences, Beijing, China.
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- **US:** United States National Herbarium, Botany Department, Smithsonian Institute, Washington, D.C., U.S.A.
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- Shigao Shan Mountain, Lingshi, Shanxi province.
- Taibai Shan Mountain, Shaanxi province.
- Wuling Shan Mountain, Xinglong, Hebei province.

Curriculum vitae

Gao Fangyou was born on October 25, 1964 in Heilongjiang province, China. After ten years of elementary and secondary education, she studied at the Northeast Forestry University, Harbin, China where she obtained BSc degree in forestry in 1985. From September 1985 to July 1988, she studied for her MSc degree in the same department. In July 1988, she defended her thesis entitled "The taxonomic study of Ulmaceae in Northeast China" and got the MSc degree in plant taxonomy in Northeast Forestry University, Harbin, China. From September 1988 to April 1997, she worked as a lecturer in the Department of Landscape (Dept. of Forestry), Beijing Agricultural College, Beijing, China. Her Ph. D. study started in May 1993 in the Department of Plant Taxonomy, Wageningen Agricultural University, the Netherlands under the supervision of Prof. Dr. L.J.G. van der Maesen. The area of research was the biosystematic study of the Rosaceous genus *Exochorda.*

Appendix I: Phytogeographic information for 22 populations of *Exochorda* investigated in China

Area: 10 × 10 m.
Coverage: c = continuous (>75%); i = interrupted (50-75%); p = parklike, in patches (25-50%); r = rare (6-25%); b = barely present, sporadic (1-5%); a = almost absent, extremely scarce (<1%) (Kent, 1992).
Species arranged according to tree, shrub, herb and alphabet.

Pop: 01
Locality: Qixia Shan Mt., Nanjiang, Jiangsu prov.
Forest type: conifer broad-leaved forest
Alt.: 150 m
Slope direction: south
Slope position: summit
Slope degree: 0°

Species	Coverage
Acer buergerianum Miq.	b
Koelreuteria paniculata Laxm.	b
Pinus massoniana Lamb.	b
Tilia miquiliana Maxim.	b
Daphne geinkwa Sieb. et Zucc.	r
Exochorda racemosa (Lindl.) Rehder subsp. *racemosa*	b
Grewia biloba G. Don	b
Ilex cornula Lindl.	b
Rosa spp.	b
Arthraxon hispidus (Thunb.) Makino	b
Atractylodes lancea DC.	b
Carex brunnea Thunb.	c
Galium aparine L	r
Leibnitzia anandria (L.) Nakai	r
Oxalis corniculata L.	p
Taraxacum mongolicum Hand.-Mazz.	b
Viola yedoensis Makino	b

Pop. 02
Locality: Chadaokou, Nanjiang, Jiangsu prov.
Forest type: bush grove
Alt.: 100 m
Slope direction: north
Slope position: foot of the mountain
Slope degree: 40°

Acer buergerianum Miq.	p
Pinus massoniana Lamb.	b
Quercus spp.	r
Carpinus spp.	b
Crataegus cuneata Sieb. & Zucc.	b
Exochorda racemosa (Lindl.) Rehder subsp. *racemosa*	p
Lonicera japonica Thunb.	b
Prunus armeniana L.	b
Rosa spp.	p
Viburnum dilatatum Thunb.	b

Artemisia spp.	b
Carex brbnea Thunb.	r
Galium aparine L.	b
Potentilla spp.	p
Viola cordifolia W. Beck	b

Pop. 03	Slope direction: south-east
Locality: Lingyan Mt., Suzhou, Jiangsu prov.	Slope position: upper slope
Forest type: conifer bush-grove	Slope degree: 30°
Alt.: 145 m	
Pinus spp.	b
Carpinus spp.	b
Celtis spp.	b
Exochorda racemosa (Lindl.) Rehder subsp. *racemosa*	r
Rosa spp.	b
Allium macrostemon Bunge	b
Arthraxon hispidus (Thunb.) Makino	b
Rubia cordifolia L.	b
Sedum aizoon L.	b

Pop. 04	Slope direction: south
Locality: Lingyan Mt., Suzhou, Jiangsu prov.	Slope position: foot of the mountain
Forest type: coniferous forest	
Alt.: 70 m	Slope degree: 40°
Acer ginnala Maxim.	b
Celtis bungeana Bl.	b
Pinus massoniana Lamb.	r
Exochorda racemosa (Lindl.) Rehder subsp. *racemosa*	b
Rosa spp.	b
Rubus spp.	b
Fern	b
Leibnitzia anandria (L.) Nakai	b
Moss	b
Oxalis corniculata L.	b

Pop. 05	Slope direction: north
Locality: Dengwei Mt., Suzhou, Jiangsu prov.	Slope position: upper slope
Forest type: conifer-bush-grove	Slope degree: 20°
Alt.: 195 m	
Quercus variabilis Bl.	r
Pinus spp.	r
Exochorda racemosa (Lindl.) Rehder subsp. *racemosa*	p
Lespedeza spp.	r
Ribes fasciculatum S. & Z. var. *chinensis* Maxim.	b

Syringa spp.	b
Carex spp.	r
Leibnitzia anandria (L.) Nakai	b

Pop. 06	Slope direction: north
Locality: Dengwei Mt., Suzhou, Jiangsu prov.	Slope position: foot of the mountain
Forest type: brush grove	
Alt.: 150 m	Slope degree: 30°
Quercus spp.	b
Camellia sinensis (L.) Kuntze.	b
Exochorda racemosa (Lindl.) Rehder subsp. *racemosa*	r
Rhododendron spp.	r
Carex spp.	p
Leibnitzia anandria (L.) Nakai	b
Smilax china L.	b

Pop. 07	Slope direction: south-east
Locality: Geling Mt., Hangzhou, Zhejiang prov.	Slope position: upper slope
Forest type: conifer-broad-leaved-forest	Slope degree: 30°
Alt.: 150 m	
Acer spp.	b
Castanea spp.	b
Pinus massoniana Lamb.	r
Exochorda racemosa (Lindl.) Rehder subsp. *racemosa*	p
Rosa spp.	b
Carex spp.	r

Pop. 08	Alt.: 200 m
Locality: ZhongTianMen, Jigong Shan Mt., Xinyan, Henan prov.	Slope direction: south
	Slope position: mountain slope
Forest type: broad-leaved-forest	Slope degree: 35°
Castanea spp.	r
Platanus acerifolia (Ait.) Willd.	b
Rhus chinensis Mill.	b
Salix spp.	b
Boomboo spp.	b
Exochorda racemosa (Lindl.) Rehder subsp. *racemosa*	r
Lespedeza spp.	b
Rubus cockburnianus Hemsl.	b
Vitex negbdo L.	b
Parthenocissus spp.	b
Arthraxon hispidus (Thunb.) Makino	b
Carex spp.	b
Elsholtzia spp.	b
Leibnitzia anandria (L.) Nakai	b

Potentilla spp.	b
Sedum spp.	r
Synurus deltoides (Ait.) Nakai	b

Pop. 09	Alt.: 710 m
Locality: Baoxiaofeng, Jigong Shan Mt., Xinyan, Henan prov.	Slope direction: south-east Slope position: upper slope
Forest type: bush-grove	Slope degree: 40°
Cuninghamia lanceolata (Lamb.) Hook.	b
Cotoneaster zabelii Schneid.	r
Exochorda racemosa (Lindl.) Rehder subsp. *racemosa*	p
Forsythia suspensa (Thunb.) Vahl	r
Rhamnus spp.	b
Rubus spp.	b
Carex spp.	r
Miscanthus sinensis Anderss.	r
Potentilla spp.	b

Pop. 10	Alt.: 630 m
Locality: Longzikou, Jigong Shan Mt., Xinyan, Henan prov.	Slope direction: north-west Slope position: mountain slope
Forest type: conifer broad-leaved-forest	Slope degree: 50°
Castanea spp.	b
Cunninghamia lanceolata (Lamb.) Hook.	b
Pinus taiwanensis Hayata	p
Pterocarya stenocarya C. DC.	b
Rhus chinensis Mill.	r
Sophora spp.	r
Deutzia spp.	b
Exochorda racemosa (Lindl.) Rehder subsp. *racemosa*	r
Forsythia suspensa (Thunb.) Vahl	b
Lespedeza spp.	b
Prunus davidiana (Carr.) Franch	b
Rhododendron simsii Planch.	b
Rosa spp.	b
Rubus spp.	b
	b
Actinidia spp.	b
Parthenocissus spp.	b
Arisaema consanguineum Schott	b
Artemisia spp.	b
Arthraxon hispidus (Thunb.) Makino	r
Galium spp.	b
Leibnitzia anandria (L.) Nakai	b
Oxalis griffithii Edgew. & Hook.f.	b
Potentilla spp.	b
Sedum spp.	b

Pop. 11	Alt.: 580 m
Locality: Longzikou to Doushiya, Jigong Shan Mt., Xinyan, Henan prov.	Slope direction: north Slope position: mountain slope
Forest type: conifer-broad-leaved-forest	Slope degree: 40°
Castanea spp.	b
Liquidambar formosana Hance	b
Pinus taiwanensis Hayata	p
Rhus chinensis Mill.	b
Sophora spp.	b
Deutzia spp.	b
Exochorda racemosa (Lindl.) Rehder subsp. *racemosa*	r
Forsythia suspensa (Thunb.) Vahl	b
Kerria japonica (L.) DC.	b
Rubus spp.	b
Parthenocissus spp.	b
Arthraxon hispidus (Thunb.) Makino	b
Fern	b
Moss	b
Polygum spp	b
Pyrrosia petiolosa (Christ) Ching	b
Sanguisorba officinalis L.	b
Sedum spp.	b

Pop. 12	Alt.: 480 m
Locality: Doushiya, Jigong Shan Mt., Xinyan, Henan prov.	Slope direction: north Slope position: upper slope
Forest type: conifer-broad-leaved-forest	Slope degree: 30°
Castanea spp.	p
Pinus taiwanensis Hayata	r
Quercus acutissima Carr.	b
Rhus chinensis Mill.	b
Exochorda racemosa (Lindl.) Rehder subsp. *racemosa*	r
Forsythia suspensa (Thunb.) Vahl	b
Kerria japonica (L.) DC.	b
Lespedeza spp.	b
Prunus pseudocerasus Lindl.	b
Rhodotypus scandens (Thunb.) Makino	b
Ulmus japonica Sagr.	b
Adenophora polyantha Nakai	b
Arthraxon hispidus (Thunb.) Makino	b
Fern	b
Galium aparine L.	b
Miscanthus floridulus (Labill.) Ward.	r

Pop. 13	Alt.: 420 m

Locality: Xianrenjing, Jigong Shan Mt., Xinyan Henan prov.	Slope direction: north
	Slope position: mountain slope
Forest type: conifer-broad-leaved-forest	Slope degree: 30°
Castanea spp.	b
Celtis bungeana Bl.	b
Cryptomeria fortunei Hooibr. ex Ott et Dietr.	b
Pinus taiwanensis Hayata	r
Rhus chinensis Mill.	p
Salix spp.	b
Sophora spp.	b
Exochorda racemosa (Lindl.) Rehder subsp. *racemosa*	r
Forsythia suspensa (Thunb.) Vahl	b
Rubus spp.	p
Clematis florida Thunb.	b
Fern	b

Pop. 14	Alt.: 110 m
Locality: Entrance, Jigong Shan Mt., Xinyan, Henan prov.	Slope direction: south
	Slope position: foot of the mountain
Forest type: deciduous-broad-leaved-forest	Slope degree: 30°
Castanea spp.	b
Koelreuteria paniculata Laxm.	b
Quercus spp.	b
Rhus chinensis Mill.	b
Acanthopanax graeilistylus W. W. Sm.	b
Campylotropis macr (Bunge) Rehder	b
Euonymus alatus (Thunb.) Sieb.	b
Exochorda racemosa (Lindl.) Rehder subsp. *racemosa*	r
Kerria japonica (L.) DC.	b
Lespedeza spp.	b
Rosa spp.	b
Rubus spp.	b
Ulmus japonica Sagr.	b
Vitex negundo L.	b
Artemisia spp.	b
Arthraxon hispidus (Thunb.) Makino	r
Carex spp.	r
Corydalis racemosa (Thunb.) Pers.	b
Duchesnea indica (Andr.) Focke	b
Equisetum arvense L.	b
Fern	b

Pop. 15	Alt.: 1020 m
Locality: Heihuguan, Taibai Shan Mt., Shaanxi prov.	Slope direction: north-west Slope position: foot of the mountain
Forest type: deciduous-broad-leaved-forest	Slope degree: 40°
Quercus spp.	b

Cotinus coggygria Scop. var. *cinerea* Engl.	p
Elaeagnus lanceolata Warb.	b
Exochorda racemosa (Lindl.) Rehder subsp. *giraldii* (Hesse) F.Y. Gao & Maesen	r
Rosa spp.	b
Spiraea spp.	p

Carex spp.	r

Pop. 16	Slope direction: south
Locality: Jiaokou, Taibai Shan Mt., Shaanxi prov.	Slope position: summit
Forest type: coniferous forest	Slope degree: 55°
Alt.: 1100 m	

Acer davidii Franch.	b
Fraxinus spp.	b
Platycladus orientalis (L.) Franch.	b

Cotinus coggygria Scop. var. *cinerea* Engl.	r
Euonymus alatus (Thunb.) Sieb.	b
Exochorda racemosa (Lindl.) Rehder subsp. *giraldii* (Hesse) F.Y. Gao & Maesen	r
Lespedeza spp.	b
Prunus spp.	b
Sambucus williamsii Hance	b
Spiraea spp.	b
Syringa spp.	b

Akebia trifoliata (Thunb.) Koidz.	b
Carex spp.	p
Lonicera maackii (Rupr.) Maxim.	b

Polygonatum sibiricum Redoute	

Pop. 17	Slope direction:
Locality: Hua Shan Mt., Shaanxi, China	Slope position: valley floor
Forest type: broad-leaved-forest	Slope degree: 0°
Alt.: 900 m	

Koelreuteria paniculata Laxm.	b

Exochorda racemosa (Lindl.) Rehder subsp. *giraldii* (Hesse) F.Y. Gao & Maesen	b
Euonymus alatus (Thunb.) Sieb.	p
Lespedeza spp.	b
Lonicera spp.	b
Myripnois dioica Bge.	b
Robinia spp.	b
Spiraea spp.	b

Akebia trifoliata (Thunb.) Koidz.	b
Celastrus orbiculatus Thunb.	b

Iris spp.	b

Pop. 18	Slope direction: south-east
Locality: Shigao Shan Mt., Shanxi prov.	Slope position: foot of the mountain
Forest type: broad-leaved-forest	
Alt.: 1140 m	Slope degree: 30°
Platycladus orientalis (L.) Franch.	b
Exochorda racemosa (Lindl). Rehder subsp. *giraldii* (Hesse) F.Y. Gao & Maesen	r
Lespedeza spp.	r
Rosa spp.	b
Vitex negundo L.	b
Carex spp.	b
Elsholtzia spp.	b

Pop. 19	Slope direction: north-east
Locality: Wuling Shan Mt., Hebei prov.	Slope position: upper slope
Forest type: conifer broad-leaved-forest	Slope degree: 30°
Alt.: 790 m	
Pinus tabulaeformis Carr.	c
Quercus liaotungensis Koidz.	b
Ulmus pumila L.	b
Exochorda racemosa (Lindl.) Rehder subsp. *serratifolia* (S .Moore) F.Y. Gao & Maesen	p
Grewia biloba Don var. *parviflora* Hand.-Mazt.	b
Lespedeza spp.	r
Prunus armeniaca var. *ansu* Maxim.	b
Rhamnus parvifolia Bge.	b
Syringa spp.	b
Vitis amurensis Rupr.	b
Carex spp.	c

Pop. 20	Slope direction: north
Locality: Fenghuang Shan Mt., Liaoning prov.	Slope position: mountain slope`
Forest type: bush grove	Slope degree: 30°
Alt.: 260 m	
Exochorda racemosa (Lindl.) Rehder subsp. *serratifolia* (S. Moore) F.Y. Gao & Maesen	c
Grewia biloba Don. var. *parviflora* Hand.-Mazt.	r
Morus australis Poir.	
Prunus armeniaca var. *ansu* Maxim.	b
Rhamnus globosa Bunge.	b
Spiraea spp.	r
Ulmus japonica Sagr.	b
Vitex negundo L.	b

Atractylodes spp.	b
Carex spp.	r
Polygonatum odoratum (Mill.) Druce	b
Potentilla anserina L.	b

Pop. 21	Slope direction: west
Locality: Haitang Shan Mt., Fuxin, Liaoning prov.	Slope position: upper slope
Forest type: bush grove	Slope degree: 25°
Alt.: 400 m	
Exochorda racemosa (Lindl.) Rehder subsp. *serratifolia* (S. Moore) F.Y. Gao & Maesen	p
Rhamnus parvifolia Bge.	b
Rhododendron spp.	r
Spiraea spp.	b
Vitex negundo L.	b
Carex spp.	r
Potentilla anserina L.	b
Scorzonera sinensis Lipsch. & Krasch.	b
Tris lactea Pall. var. *chinensis* (Fisch.) Koidz	b

Pop. 22	Slope direction: north
Locality: Haitang Shan Mt., Fuxin, Liaoning prov.	Slope position: mountain slope
Forest type: bush grove	Slope degree: <30°
Alt.: 380 m	
Acer mono Maxim.	b
Pinus tabulaeformis Carr.	r
Ulmus japonica Sagr.	b
Exochorda racemosa (Lindl.) Rehder subsp. *serratifolia* (S. Moore) F.Y. Gao & Maesen	r
Rhamnus parvifolia Bge.	b
Adenophora spp.	b
Carex spp.	r
Orobanche pycnostachya Hance	b
Polygonatum odoratum (Mill.) Druce	b
Potentilla spp.	b
Scorzonera sinensis Lipsch. & Krasch.	b
Sedum spp.	b
Iris lactea Pall. var. *chinensis* (Fisch.) Koidz.	b

Appendix II: *Exochorda*: Cultivation and propagation

Outside its native China and Central Asia, the handsome ornamental bush *Exochorda* is found occasionally in Botanical Gardens, and in private gardens it is probably rather rare. Very few nurseries offer the shrubs for sale, these are mainly located in Boskoop, the Netherlands. 'The Bride' is sold by several nurseries, particularly in Boskoop, Dedemsvaart, Zeist, Kapel-Avezaath, Velserbroek, Schimmert (the Netherlands), and Kalmthout, Brugge and Mol (Belgium).

The most conspicuous about *Exochorda* is its flowering. The flowers are 2.5-4.5 cm in diameter and show white, and 3 to 12 are placed together in racemes. Cultivar 'The Bride' has pendulous branches. The English name pearl bush is very apt, at least during the bud stage, because the flower buds present themselves as shiny pearls along the peduncles. Flowering is in April-May in the northern hemisphere, after the leaves have sprouted. The number of stamens varies between 9 and 37, normally 15 and 30. In one plant either the pistils or the stamens are well-developed, rendering the plants functionally dioecious. In functionally female plants the fruits develop into bony-lignified brown fruits of c. 1 cm diameter with 5 locules, each containing 2 flat brown winged seeds. The fruits remain fixed on the shrub for quite a long time, so at flowering the previous years' fruits are sometimes still present. The five locules remain together and appear similar to star aniseed.

Exochorda leaf margins are usually entire, but sometimes serrate, there is even quite a discrepancy between leaves on the same plant. The petiole of 5-25 mm has two early deciduous stipules (*Spiraea* usually has no stipules at all). The shrubs are green, but sometimes the leaf petioles and the young twigs are reddish. This additional colour is not spectacular.

In the Botanic Gardens in Wageningen many *Exochorda* shrubs have been planted, from nurseries as well as of wild origin. Particularly the plants from cultivation are difficult to name. This is not surprising for a species that is functionally dioecious, so all seeds originate from cross-fertilization. When two shrubs of different subspecies are growing side by side, the harvested seed is hybrid. The plants of wild origin are easier to name, but the differences are small, and therefore *Exochorda* is now considered as one species with some slightly different geographically separated populations.

It is not a surprise that the treatment of the genus in the Flora of China (1974) is identical with Rehder's treatment for the cultivated plants in the collection of the Arnold Arboretum, and this seems artificial at the least. A revision of *Exochorda* has only been possible from plants collected from the wild, and this material has now become available. The Wageningen Botanic Gardens (1997-1998) have several new Chinese populations of wild origin in her nursery, that may become available in the near future.

The cultivation of *Exochorda* is rather difficult. Repeatedly entire branches die off, and sometimes even the whole shrub wilts. Hence, as a solitary shrub most *Exochorda* are less suitable. In a mixed shrub plantation the species may perform excellently. The shrubs may grow to 3 m tall (in the Belmonte Arboretum a specimen of subsp. *giraldii* even reached 5

m) and its habit is multi-stemmed, open, ascending or sometimes somewhat pendant. Apart from the wilting disease there are no problems. *Exochorda* has no specific preference for soil type, supports chalk (except *E. racemosa*), and appreciates some sunshine. Pruning is supported well, and the shortening of the flowering branches promotes the next flowering. A cultivar suitable for solitary placement is 'The Bride', a richly flowering, relatively low spreading shrub (to 1.75 m) with pending branches, selected by the Grootendorst company in Boskoop (in 1938). This cultivar is functionally female, very appropriate for a bride. 'The Bride' is a selection from a hybrid that originated soon after 1900 in Nancy at the nursery of Lemoine from a cross between *E. korolkowii* as female with *E. racemosa* as male parent. Another named cultivar in *Exochorda* is 'Irish Pearl', a hybrid between *E. giraldii* var. *wilsonii* and *E. racemosa*, that was obtained in the Botanic Garden of Glasnevin, and that was characterized by very long flowering branches. This cultivar seems to have disappeared from cultivation, it has not been possible to obtain it for the collection in Wageningen, even not from Glasnevin. A third cultivar listed is subsp. *serratifolia* 'Snow White' (Esveld, 1997) with the purest white flowers.

Exochorda can be propagated well from seed, but as said before does not breed true to species at all. Production is time-consuming this way, hence it has not caught on. vegetative propagation is possible from half-ripened cuttings with soil heat provided; the use of suckers is also very suitable, again with some soil heat. Especially subsp. *racemosa* forms suckers, that can also be used as root cuttings. Experimentation in this field may result in a more efficient propagation.

There is certainly scope for improvement and further selection in this genus, to make it more popular. The pure white flowers of *Exochorda* are quite beautiful, and worth waiting for every springtime.

References: Doorenbos, J. 1997. pers. comm.; Esveld, C. 1997. Catalogus 97/99: 138. Hart, S. 1995. Plantenvinder voor de lage landen, Terra, Warnsveld; Huxley, A. 1992. RHS Dictionary. P. 274; Philip, C. & Lord, T. 1988 etc. The Plant Finder, West Ewell: Hardy Plant Society, West Ewell; Wijnands, D.O. 1993. pers. comm.

Appendix III: Climatic conditions in the main distribution areas of *Exochorda* in China, Central Asia and in the Netherlands

Areas	Climatic features	Average temperature °C		Average annual rainfall (mm)	
		Jan	July		
Hebei prov.	temperate continental climate	-14.0 – -2.0	20.0 – 27.0	400 – 800	
Henan prov.	warm-temperate/semi-humid & subtropical/humid climate	-3.0 – 3.0	24.0 – 29.0	500 – 900	50% of the rains falls during summer
Liaoning prov.	temperate & subtropical monsoonal climate	-17.0 – -5.0	21.0 – 25.0	400 – 1200	60% of the rain falls from June to Aug.
Shaanxi prov.	temperate & subtropical monsoonal climate	-11.0 – 3.5	21.0 – 28.0	400 – 1000	most of the rain falls from July to Sept.
Shanxi prov.	temperate continental climate	-16.0 – -2.0	19.0 – 28.0	350 – 700	60% of the rain falls during summer
Shanghai-NanjingRegion	warm-temperate/semi-humid & subtropical/humid climate	-2.0 – 4.0	26.0 – 29.0	800 – 1200	60% of the rain falls during summer
Zhejiang prov.	subtropical monsoonal climate	2.0 – 8.0	27.0 – 30.0	850 – 1700	
Kirghizstan	temperate continental climate	-14.0 – -5.0	16.0 – 27.0	200 – 1000	
Tadzhikistan	temperate continental climate			150 – 700	
Uzbekistan	continental climate			800 – 1000	
Netherlands	Sea climate	1.5 – 2.0	17.0 – 17.5	750 – 800	

Sources: Atlas of the People's Republic of China (1995) and Atlas of the world (1981).

Index of plant names

New names and the page number of main entries for plant names are in **bold face**. Synonyms, nomina nuda are given in *italics*.