

Systematics and floral evolution in *Fraxinus* (Oleaceae)

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Summary – The genus *Fraxinus* is one of 24 genera in the family Oleaceae. *Fraxinus* currently consists of 48 accepted tree and shrubby species distributed from the tropics to temperate regions of the northern hemisphere. About one third of the species is insect-pollinated and has small, white, scented flowers borne many together in showy terminal panicles. The other two thirds are wind-pollinated, with apetalous and usually unisexual flowers borne in tight lateral panicles or racemes. Unisexual flowers have evolved on three separate occasions from bisexual ones in wind-pollinated species.

The genus is divided into six sections: *Fraxinus*, *Sciadhanthus*, *Pauciflorae*, *Melioides*, *Ornus* and *Dipetalae*. These sections contain 45 species plus a few recognised subspecies. Three species are unclassified due to uncertain positions in the phylogenetic tree. This latest classification of the genus is based on an updated version of WALLANDER'S (2008) phylogenetic tree, which is based both on molecular and morphological data. A key to the sections is given as well as a systematic table with all accepted taxa, common synonyms and geographic distribution. Each section is presented along with some common, botanically interesting or commercially important species.

OLEACEAE, THE OLIVE FAMILY

Oleaceae is a family of about 600 species in 24 extant genera (WALLANDER & ALBERT 2000). They occur all over the world in tropical, subtropical and temperate climates. Phylogenetically, the family is near the base in the order Lamiales. The largest genus in the family is *Jasminum* with about 200 species. Other well-known genera in the family are *Forsythia* (11 spp.), *Ligustrum* (45 spp.), *Syringa* (20 spp.), *Olea* (40+ spp.) and *Fraxinus*.

The species are trees, shrubs or woody climbers with opposite, simple or compound leaves without stipules. The flowers are hypogynous (petals and sepals attached under the ovary) and four-merous, generally with two stamens, but four stamens occur in some species. The corolla is actinomorphic (radial symmetric) and usually sympetalous. Free petals

occur in *Chionanthus* and *Fraxinus*, and apetalous flowers occur in *Nestegis*, *Forestiera*, and wind-pollinated species of *Fraxinus*. The ovary is syncarpous (carpels fused), consisting of two carpels. Fruit types range from loculicidal capsules (with two locules), woody schizocarps (a dry fruit type that splits in two parts), and samaras to berries and drupes.

Most of the species in the family are insect-pollinated with petaliferous, fragrant and nectariferous flowers (e.g. *Jasminum*, *Forsythia*, *Ligustrum*, *Syringa*, *Chionanthus*). Six of the genera in the family contain species with wind-pollinated flowers (*Fraxinus*, *Forestiera*, *Priogymnanthus*, *Nestegis*, *Phillyrea* and *Olea*).

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These have no corolla, or a reduced open corolla, with no nectar or fragrance. A calyx may be present or not. Some species are both wind- and insect-pollinated (e.g. species of *Olea* and *Fraxinus*).

THE GENUS *FRAXINUS*, THE ASH TREES

Since LINNAEUS described the genus *Fraxinus* in 1753, almost 800 taxa (species, subspecies and varieties) have been described. Obviously most of these are synonyms and WALLANDER (2008) accepted 43 species. Later, five more American and one Chinese species were accepted and two Asian species merged into one so currently there are 48 accepted species (table 1).

The species of *Fraxinus* are distributed around the northern hemisphere, from tropical to temperate climates. The two main centres of distribution are North America and China. They are mostly large or small trees, but some shrubby species occur mainly in arid areas. The leaves are characteristically oddly pinnately compound but a few species or subspecies have simple leaves by reduction (*F. anomala*²⁾). All species are deciduous except *F. griffithii* and *F. uhdei* which are evergreen or

semi-evergreen in tropical climates. The flowers are borne in panicles or rarely racemes. They have four (rarely two), free (united in two species), linear petals and a small synsepalous calyx. In wind-pollinated flowers the petals or both petals and calyx are missing. The fruit is a samara, normally one-seeded.

Fraxinus contains both wind- and insect-pollinated species and the breeding systems range from hermaphrodites via androdioecious and polygamous to dioecious species (see Box 1). Thirty-four species are wind-pollinated and dioecy has evolved on three separate occasions after the evolution of wind-pollination (WALLANDER 2001, 2008). Dioecy evolved once via androdioecy and twice via polygamy as intermediate steps [Ill. 1]. Some of the 14 insect-pollinated species might in fact be both wind- and insect-pollinated, as evidenced by the protruding anthers and copious pollen production. Many of them are androdioecious, and it is hypothesised that this was an important prerequisite in the evolution of wind-pollination with loss of corolla and later completed unisexuality (WALLANDER 2001). Androdioecy is a very rare breeding system elsewhere among angiosperms but in Oleaceae and in particular *Fraxinus* there are many androdioecious species (WALLANDER 2001).

Box 1. Explanation of different breeding systems that occur in *Fraxinus*.

Hermaphroditism: all trees have only bisexual (hermaphrodite) flowers

Androdioecy: separate male trees (with only male flowers) and hermaphrodite trees (with only bisexual flowers)

Andromonoecy: only one type of tree with both unisexual male and bisexual flowers

Polygamy: a mixture of trees with only male, or only female, or only hermaphrodite flowers, or trees with mixed unisexual and bisexual flowers in the same or different inflorescences

Dioecy: separate male trees (with only male flowers) and female trees (with only female flowers)

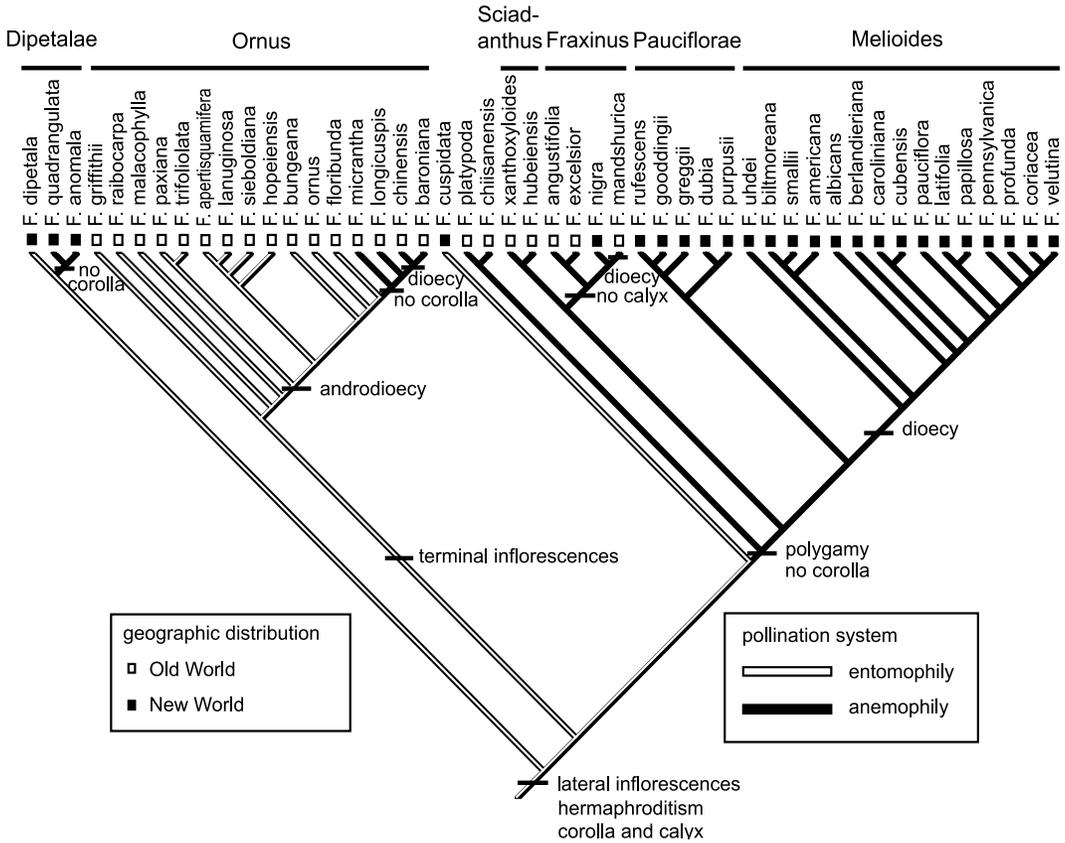
²⁾ Authors of all species names mentioned in the text are given in table 1.

Table 1. – Revised infrageneric classification of *Fraxinus* (Oleaceae) listing the 48 accepted species and 3 subspecies, their geographical distribution and common synonyms. Based on Table 2 in WALLANDER (2008).

Sections and species	Geographic distribution	Synonyms
Section <i>Dipetala</i> (Lingelsh.) E. Nikolaev		
<i>F. anomala</i> Torr. ex S. Wats.	SW USA, C Mexico	<i>F. lowellii</i> Sarg., <i>F. potosina</i> T. S. Brandeg.
<i>F. dipetala</i> Hook. & Arn.	SW USA, NW Mexico	<i>F. jonesii</i> Lingelsh., <i>F. parryi</i> Moran, <i>F. trifoliata</i> (Torr.) Lewis & Epling
<i>F. quadrangulata</i> Michx.	C & E USA, C Canada	
Section <i>Fraxinus</i>		
<i>F. angustifolia</i> Vahl subsp. <i>angustifolia</i>	SW Europe, NW Africa	
<i>F. angustifolia</i> Vahl subsp. <i>oxycarpa</i> (Willd.) Franco & Rocha Afonso	SE & C Europe	<i>F. oxycarpa</i> Willd., <i>F. oxyphylla</i> M. Bieb. (nom. illeg.), <i>F. pallisiae</i> A. J. Willmott
<i>F. angustifolia</i> Vahl subsp. <i>syriaca</i> (Boiss.) Yalt.	Turkey to Central Asia	<i>F. syriaca</i> Boiss., <i>F. potamophila</i> Herder, <i>F. sogdiana</i> Bunge, <i>F. turkestanica</i> Carr.
<i>F. excelsior</i> L.	N & C Europe to W Russia and around the Black Sea	<i>F. coriariifolia</i> Scheele
<i>F. mandshurica</i> Rupr.	China, Japan, Korea, E Russia	<i>F. nigra</i> Marsh. subsp. <i>mandshurica</i> (Rupr.) S. S. Sun
<i>F. nigra</i> Marsh.	E USA, SE Canada	<i>F. sambucifolia</i> Lam.
Section <i>Malioides</i> (Endl.) Lingelsh.		
<i>F. albicans</i> Buckl.	SW USA (Texas, Oklahoma), N Mexico	<i>F. texensis</i> (Gray) Sarg., <i>F. americana</i> L. var. <i>texensis</i> A. Gray, <i>F. americana</i> L. subsp. <i>texensis</i> (Gray) G. N. Miller
<i>F. americana</i> L.	E USA & SE Canada	
<i>F. berlandieriana</i> DC.	SW USA, NE, C & E Mexico	<i>F. americana</i> L. var. <i>berlandieriana</i> (DC.) Wesmael, <i>F. pubescens</i> Lam. var. <i>berlandieriana</i> (DC.) Wenz., <i>F. pubescens</i> Lam. var. <i>hndheimeri</i> Wenz., <i>F. tritalata</i> Buckl., <i>F. viridis</i> Michx. var. <i>berlandieriana</i> (DC.) A. Gray, <i>F. viridis</i> Michx. f. <i>berlandieriana</i> (DC.) Voss, <i>F. viridis</i> Michx. var. <i>tritalata</i> (Buckley) Schelle
<i>F. biltmoreana</i> Beadle	E USA	<i>F. americana</i> L. var. <i>biltmoreana</i> (Beadle) J. Wright
<i>F. caroliniana</i> Mill.	SE USA	<i>F. platycarpa</i> Michx., <i>F. triptera</i> Nutt., <i>F. rebdieriana</i> Lingelsh.
<i>F. coriacea</i> S. Wats.	SW USA, NW Mexico	<i>F. velutina</i> var. <i>coriacea</i> (S. Wats.) Rehd., <i>F. pistaciaefolia</i> Torr. var. <i>coriacea</i> (S. Wats.)
<i>F. cubensis</i> Griseb.	SE USA (S Florida), Cuba	<i>F. caroliniana</i> Mill. var. <i>cubensis</i> (Griseb.) Lingelsh., <i>F. caroliniana</i> Mill. subsp. <i>cubensis</i> (Griseb.) Borh., <i>F. pennsylvanica</i> Marsh. var. <i>cubensis</i> (Griseb.) E. Murray
<i>F. latifolia</i> Benth.	W USA, SW Canada	<i>F. oregana</i> Nutt., <i>F. pennsylvanica</i> Marsh. subsp. <i>oregana</i> (Wesmael) Mill.

Sections and species	Geographic distribution	Synonyms
<i>F. papillosa</i> Lingelsh.	SW USA, N Mexico	
<i>F. pauciflora</i> Nutt.	SE USA	<i>F. floridana</i> (Wenzig) Sarg., <i>F. hybrida</i> Lingelsh., <i>F. profunda</i> var. <i>asbei</i> E. J. Palmer
<i>F. pennsylvanica</i> Marsh.	C & E USA, S Canada	<i>F. lanceolata</i> Borkh., <i>F. pubescens</i> Lam., <i>F. tomentosa</i> Michx. f. (nom. rej.)
<i>F. profunda</i> (Bush) Bush	E USA, Canada	<i>F. michauxii</i> Britt., <i>F. americana</i> L. var. <i>profunda</i> Bush, <i>F. pennsylvanica</i> Marsh. var. <i>profunda</i> (Bush) Sudworth, <i>F. pennsylvanica</i> Marsh. subsp. <i>profunda</i> (Bush) A. E. Murray
<i>F. smallii</i> Britt.	E USA	<i>F. americana</i> L. var. <i>coriacea</i> Sarg.
<i>F. uhdeti</i> (Wenzig) Lingelsh.	C America, Hawaii, cult.	<i>F. americana</i> L. var. <i>uhdeti</i> Wenzig, <i>F. caevikiana</i> Standley & Steyer., <i>F. chiapensis</i> Lundell, <i>F. hondurensis</i> Standley
<i>F. velutina</i> Torr.	SW USA, N & C Mexico	<i>F. pennsylvanica</i> Marsh. subsp. <i>velutina</i> (Torr.) G. N. Miller, <i>F. attenuata</i> M. E. Jones, <i>F. pistaciaefolia</i> Torr., <i>F. standleyi</i> Rehd., <i>F. toumeyii</i> Britt.
Section <i>Ornus</i> (Boehm.) DC.		
<i>F. apertisquamifera</i> Hara	Japan	
<i>F. baroniana</i> Diels	China	
<i>F. bungeana</i> DC.	China	
<i>F. chinensis</i> Roxb. subsp. <i>chinensis</i>	China, Korea, Vietnam, Thailand	<i>F. caudata</i> J. L. Wu, <i>F. lingsheimii</i> Rehder, <i>F. medicinalis</i> S. S. Sun, <i>F. rhynchophylla</i> Hance var. <i>huashanensis</i> J. L. Wu & Z. W. Xie, <i>F. sargentiana</i> Lingelsh., <i>F. szaboana</i> Lingelsh., <i>F. yunnanensis</i> Lingelsh.
<i>F. chinensis</i> Roxb. subsp. <i>rhynchophylla</i> (Hance) E. Murray	N China, Korea, Japan, SE Russia	<i>F. rhynchophylla</i> Hance, <i>F. japonica</i> Blume ex K. Koch
<i>F. floribunda</i> Wall.	Afghanistan through Himalaya to SE Asia	<i>F. insularis</i> Hemsl., <i>F. retusa</i> Champ. ex Benth., <i>F. odontocalyx</i> Hand.-Mazz., <i>F. stylosa</i> Lingelsh., <i>F. fallax</i> Lingelsh.
<i>F. griffithii</i> C. B. Clarke	SE Asia	<i>F. ferruginea</i> Lingelsh., <i>F. formosana</i> Hayata, <i>F. philippinensis</i> Merr., <i>F. bracteata</i> Hemsley, <i>F. gultinensis</i> S.K. Lee & F.N. Wei
<i>F. bopetensis</i> Tang	China	<i>F. rhynchophylla</i> var. <i>bopetensis</i> (Tang) Chü ex J.Z. Liu
<i>F. lanuginosa</i> Koidz.	Japan	
<i>F. longicauspis</i> Sieb. & Zucc.	Japan	
<i>F. malacophylla</i> Hemsl.	China, Thailand	<i>F. borealis</i> Nakai
<i>F. micrantha</i> Lingelsh.	Himalaya	<i>F. retusifoliolata</i> Feng ex P.Y. Bai
<i>F. ornus</i> L.	C & E Mediterranean, SW Asia	

Sections and species	Geographic distribution	Synonyms
<i>F. paxiana</i> Lingelsh.	Himalaya, China	<i>F. sikkimensis</i> (Lingelsh.) Hand.-Mazz., <i>F. suaveolens</i> W.W. Smith, <i>F. depauperata</i> (Lingelsh.) Z. Wei
<i>F. railocarpa</i> Regel	C Asia	
<i>F. sieboldiana</i> Blume	China, Japan, Korea	<i>F. mariesii</i> Hook. f.
<i>F. trifoliolata</i> W. W. Smith	China	<i>F. punctata</i> S. Y. Hu
Section <i>Pauciflorae</i> (Lingelsh.) E. Wallander		
<i>F. dabia</i> (Willd. ex Schult. & Schult. f.) P. S. Green & M. Nee	E Mexico, Guatemala	<i>F. petenensis</i> Lundell, <i>F. schiedeana</i> Schlecht. & Cham.
<i>F. gooddingii</i> Little	SW USA (Arizona), N Mexico (Sonora)	
<i>F. greggii</i> A. Gray	SW USA (Texas), NE & C Mexico	<i>F. nummularis</i> M. E. Jones, <i>F. schiedeana</i> Schlecht. & Cham. var. <i>parviflora</i> Torr.
<i>F. purpusii</i> Brandegee	NE & C Mexico, Guatemala	<i>F. bicolor</i> Standley & Steyerin., <i>F. velleera</i> Standley & Steyerin.
<i>F. rufescens</i> Lingelsh.	C Mexico	
Section <i>Sciadanibus</i> (Coss. et Dur.) Lingelsh.		
<i>F. habietenis</i> S. Z. Qu, C. B. Shang & P. L. Su	China	
<i>F. xanthoxyloides</i> (G. Don) Wall. ex DC.	NW Africa, Himalaya	<i>F. dimorpha</i> Coss. & Dur.
<i>Incertae sedis</i>		
<i>F. cuspidata</i> Torr.	SW USA, N Mexico	<i>F. macropetala</i> Eastw.
<i>F. chiisanensis</i> Nakai	Korea	
<i>F. platypoda</i> Oliv.	China, Japan	<i>F. spaethiana</i> Lingelsh.



1 – Phylogeny of *Fraxinus* based on molecular and morphological data with some morphological traits mapped on the tree. [E. Wallander]

PHYLOGENY AND CLASSIFICATION

A nearly complete phylogeny of the genus *Fraxinus* was reconstructed based on molecular and morphological data (WALLANDER 2008) and updated for the present article with some missing species (WALLANDER, unpublished data), see Ill. 1. The genus is clearly monophyletic and has strong molecular support.

The genus *Fraxinus* is classified into six sections (WALLANDER 2008): *Fraxinus*, *Sciadanthus*, *Pauciflorae*, *Melioides*, *Ornus* and *Dipetalae* (table 1). These sections contain 45 species and a few subspecies. Three species are unclassified (*incertae sedis*) due to uncertain positions in the phylogenetic tree. The sec-

tional key below (updated from WALLANDER 2008) gives the diagnostic characters of the sections. More information is given for the sections and some species in each section further below. A vegetative key to cultivated species of *Fraxinus* in Western Europe is given by DE LANGHE (2012).

SECTIONAL KEY

This key to the sections of *Fraxinus* does not cover the two unplaced species *F. platypoda* and *F. chiisanensis* (some of their traits are found in both the sections *Melioides* and *Fraxinus*).

1. Inflorescences emerging with the leaves on current year shoots from terminal buds; flowers with 4, free, white petals, or apetalous, always with calyx; hermaphrodites, androdioecious or dioecious; 16 Old World species section *Ornus*
1. Inflorescences emerging from lateral buds on previous year's shoot, before or at the same time as the leaves emerge from terminal buds; flowers with 2-4 united petals or apetalous, with or without calyx; hermaphrodites, polygamous, or dioecious; New World or Old World species
 2. Stems quadrangular; flowers mostly bisexual, with 2 united petals or without petals; 3 New World species section *Dipetalae*
 2. Stems terete; flowers uni- or bisexual, with 4 united petals or without petals; New World or Old World species
 3. Corolla with 4 united petals; 1 New World species *F. cuspidata*
 3. Flowers without petals; New World or Old World species
 4. Shrubs or small trees; leaf rachis ± winged; flowers with calyx; polygamous
 5. Few-flowered, cymose panicles; samaras small (1.5-2.5 cm); 5 New World species section *Pauciflorae*
 5. Many-flowered and dense, cymose panicles; samaras large (3-5 cm); 2 Old World species section *Sciadanthus*
 4. Mostly large trees; leaf rachis not winged; flowers with or without calyx; dioecious or polygamous
 6. Flowers without calyx or with small and/or deciduous calyx; polygamous or dioecious with rudimentary stamens; seed cavity of samara flattened; 3 Old World and 1 New World species section *Fraxinus*
 6. Flowers with calyx; strictly dioecious; seed cavity of samara terete or flattened; 15 New World species section *Melioides*

SECTION *FRAXINUS*

The section *Fraxinus* comprises four species; one American (*F. nigra*), two mainly European (*F. excelsior* and *F. angustifolia*) and one East Asian species (*F. mandshurica*). They are all relatively large and wind-pollinated trees. The species of this section are either polygamous (*F. nigra* and *F. excelsior*), andromonoecious (*F. angustifolia*) or dioecious (*F. mandshurica*). The male flowers consist of two stamens, the hermaphrodite flowers of one pistil and two stamens, and the female flowers of one pistil and more or less rudimentary stamens. The flowers are without a calyx, or have a reduced or deciduous calyx. They are distinguished from the strictly dioecious species of the section *Melioides* in having a flattened seed cavity of the samara (versus terete in the section *Melioides*) and foliar terminal bud scales (versus entire in the section *Melioides*).

In Europe, the Common ash *F. excelsior* [Ill. 2a-c] is the most common and well-known species. It is a large tree (normally up to 35 m but even taller trees up to 46 m can be found) distributed in central and northern Europe and commercially important in central Europe. In the last decade, however, an ash disease caused by the fungus *Chalara fraxinea* (PAUTASSO *et al.* 2013) has spread fast, affecting its survival and future use. The flowers are either male, hermaphrodite or female and normally occur in sexually pure inflorescences, but mixes of male and hermaphrodite flowers are not uncommon. Female flowers may have a continuum of more or less rudimentary stamens, ranging from functionally female to hermaphrodite. The species has therefore been termed polygamous but recent research has shown that it is functionally dioecious (FRAXIGEN 2005, BOCHENEK & ERIKSEN 2010, BOCHENEK 2011). The protogynous



2 – (a) Male inflorescences (panicles) of *Fraxinus excelsior* shedding pollen in spring, (b) female inflorescences with rudimentary stamens, and (c) foliage with young and green fruits (samaras) in early summer. Göteborg, Sweden [E. Wallander, 6-05-2006, 6-05-2006 & 5-06-1997]



3 – (a) Hermaphrodite flowers of *Fraxinus angustifolia* in a raceme (as opposed to *F. excelsior*'s panicle) and (b) leaves with narrow and serrate leaflets. Göteborg, Sweden [E. Wallander, 4-05-1995] and Ronda, Spain [E. Wallander, 31-03-2000]

hermaphrodite flowers have stamens with fertile pollen but are rendered functionally female because the pollen of pure male trees is released earlier and thus outcompete the later hermaphrodite pollen in cross-pollinations on other females and hermaphrodites. However, hermaphrodites can successfully self-pollinate if no male trees are in the vicinity.

Fraxinus angustifolia, the Narrow-leaved ash, includes a complex of taxa that have not yet been fully clarified due to large variation in morphology. Three geographical subspecies are recognised: *F. angustifolia* subsp. *angustifolia* in southwestern Europe and northwestern Africa, *F. angustifolia* subsp. *oxycarpa* in southeastern and central Europe and *F. angustifolia* subsp. *syriaca* from Turkey to Central Asia. The trees can reach over 30 m in height. The leaflets are relatively narrow with a distinct serrate or toothed margin [Ill. 3b] but leaf and shoot pubescence and leaflet morphology within this complex is too variable to deserve specific recognition. Therefore *F. pallisiae* [Ill. 4], with pubescent leaves and shoot, is treated as a synonym of *F. angustifolia* subsp. *oxycarpa*. *Fraxinus potamophila* and *F. sogdiana* in the Turkestan region are treated as synonyms of *F. angustifolia* subsp. *syriaca* but more studies are needed to confirm their status. *Fraxinus*



4 – *Fraxinus pallisiae*, with pubescent leaves and shoots, is treated as a synonym of *F. angustifolia* subsp. *oxycarpa*. In *F. angustifolia* it is common to find buds and leaves in whorls of three instead of opposite. Von Gimborn Arboretum, The Netherlands [E. Wallander, 6-10-2012]

angustifolia differs morphologically from *F. excelsior* and is andromonoecious (FRAXIGEN 2005). In contrast to all other taxa of the genus, which have compound paniculate inflorescences, *F. angustifolia* (including all its synonyms) has simple, unbranched racemes [Ill. 3a]. Also, it usually has leaves and buds in whorls of three [Ill. 4] instead of the normal opposite leaves. The bud colour is brown contrasting to the black colour of *F. excelsior* buds. Additional characters for distinguishing between *F. angustifolia* and *F. excelsior* are listed



5 – (a) Female flowers of *Fraxinus mandshurica*, with rudimentary anthers. (b) The leaves are relatively large, up to 40 cm long, with conspicuous tufts of rufous hair where the leaflets attach to the rachis. Göteborg Botanical Garden, Sweden [E. Wallander, 8-05-2000 & 2-07-1997]

by FRAXIGEN (2005). *Fraxinus angustifolia* is closely related to *F. excelsior* and they have also been shown to be able to hybridise (RAQUIN *et al.* 2002, FERNANDEZ-MANJARRES *et al.* 2006, HEUERTZ *et al.* 2006).

The Manchurian ash *F. mandshurica* is a large (up to 30 m), commercially important, timber tree in eastern Asia (China, eastern Russia, Japan and Korea). It is dioecious with anther rudiments in female flowers [Ill. 5a]. It is most closely related to *F. nigra* (Black ash) in eastern North America [Ill. 6].

SECTION *SCIADANTHUS*

The section *Sciadanthus*, which is sister to the section *Fraxinus*, consists of only two Old World species: *F. xanthoxyloides* [Ill. 7], distributed from Morocco and Algeria through the Middle East to the Himalayas, and *F. hubeiensis*, which is a threatened species endemic to the Hubei province in China. They are both relatively small trees or shrubs, and characterised by apetalous flowers with calyx, except that the male flowers of *F. xanthoxyloides* lack calyx. The flowers are polygamous and wind-pollinated. They resemble the New World *Pauciflorae*, but have many more flow-



6 – Leaves of *Fraxinus nigra*, which is closely related to *F. mandshurica*. [K. Kanoti, Maine Forest Service, Bugwood.org]

ers in their congested, cymose panicles, and larger samaras. The leaves are relatively small (7-15 cm) with a more or less winged leaf-rachis. Compared to the next section the samaras are in larger clusters.



7 – (a) A hermaphrodite inflorescence of *Fraxinus xanthoxyloides* and (b) its foliage with small compound leaves. Göteborg Botanical Garden, Sweden [E. Wallander, 28-04-2004 & 26-06-1997]

SECTION *PAUCIFLORAE*

The section *Pauciflorae* consists of five New World species that occur in arid regions of southwestern USA, Mexico, and Guatemala. They are shrubs or small trees with small coriaceous leaves. In common with the two species of section *Sciadanthus*, the leaves have winged rachises, but in contrast they have few-flowered panicles [Ill. 8b]. The flowers are polygamous, apetalous, and wind-pollinated. The samaras are relatively small and have a persistent calyx.

Fraxinus greggii (Gregg's ash, or Littleleaf ash) [Ill. 8a-b], occurring in Texas and north-eastern and central Mexico, is closely related to *F. gooddingii* (restricted to Arizona in USA and Sonora in Mexico) and *F. rufescens* (in



8 – (a) *Fraxinus greggii* has small pinnate leaves and occurs in Texas and Mexico. (b) The flowers are apetalous.

JC Raulston Arboretum at NC State University, USA [M. Weathington, 11-07-2008 & T. Alderton, 25-03-2011]

central Mexico). The other two, *F. dubia* and *F. purpusii*, occur in Mexico and Guatemala. Except for *F. greggii*, the species in this section are poorly known and especially the latter two species are in need of a deeper study.

SECTION *MELIOIDES*

The section *Melioides* contains 15 American species. They are all medium-sized to large dioecious trees. The unisexual flowers are apetalous and wind-pollinated. The female flowers consist of a calyx and one pistil, and the male flowers of two stamens with elongated anthers and a small calyx. There are no rudimentary organs of the opposite sex in the flowers [Ill. 13b]. The calyx is persistent in the samaras, which have a distinctly terete seed cavity in most species (more flattened in *F. caroliniana* and *F. pauciflora*). The wing may be decurrent along the seed cavity or not.

The species can roughly be divided into two geographical groups (not a phylogenetical division). The western and southwestern species are *F. albicans* (Texas ash) [Ill. 9], *F. berlandieriana* (Mexican ash), *F. coriacea* (Leather-leaved ash, Ill. 10a), *F. latifolia* (Oregon ash) [Ill. 11a], *F. papillosa* (Chihuahuan ash) and *F. velutina* (Desert ash) [Ill. 10b]. This group can also include *F. uhdei* (Tropical ash) [Ill. 12] which is distributed in Central America and cultivated in the Neotropics. The eastern and southeastern species are *F. americana* (White ash), *F. smallii* (Small's ash), *F. biltmoreana* (Biltmore ash), *F. caroliniana* (Water ash), *F. cubensis* (Cuban water ash), *F. pauciflora* (Swamp ash), *F. pennsylvanica* (Green ash, Red ash) [Ill. 13] and *F. profunda* (Pumpkin ash) [Ill. 11b].

Fraxinus albicans [Ill. 9] is the correct name for the Texas ash previously known as *F. texensis* (NESOM 2010b). In USA it occurs only in Texas and Oklahoma and in northern Mexico.

SYSTEMATICS AND FLORAL EVOLUTION IN *FRAXINUS* (OLEACEAE)



9 – *Fraxinus albicans* is a small tree distributed in Texas and Oklahoma in USA and northern Mexico. It has 3-5 long-petiolulate and ovate leaflets. Texas, USA [E. Wallander, 12-08-1999]



10 – (a) *Fraxinus coriacea* and (b) *F. velutina* are both distributed in southwestern USA and northern Mexico. The leaflets are more leathery and thick in *F. coriacea* which also has a more eastern distribution in the USA from Utah to Texas. Arboretum Wespelaar, Belgium [E. Wallander, 7-10-2012]



11 – (a) *Fraxinus latifolia* with its sessile and hairy leaflets is distributed in western USA. (b) *Fraxinus profunda* is hexaploid and the relatively large leaves and the whole shoot is velvety hairy. It occurs in wet areas of southeastern USA. Von Gimborn Arboretum, The Netherlands [E. Wallander, 6-10-2012]

Fraxinus coriacea [Ill. 10a] has been treated as a variety of *F. latifolia* [Ill. 11a] and of *F. velutina* [Ill. 10b] until NESOM (2010c) recognised it at specific rank. The three species occur in different parts of western USA and northern Mexico.

Fraxinus uhdei, the Tropical or Shamel ash [Ill. 12], is a large semi-evergreen tree that occurs naturally from central Mexico to Guatemala (FRANCIS 1990). It has also been introduced into cultivation or as a street tree in Costa Rica, in northern parts of the Andes (Colombia and Venezuela), on Puerto Rico and Hawaii. There has been some confusion about the name of the cultivated species. For some unknown reason it was thought to be *F. chinensis* in the Andes but has now been verified as *F. uhdei* (WALLANDER, personal observation and unpublished data).

The *Melioides* contains some polyploid species complexes. *F. americana* is diploid, *F. smallii* is tetraploid and *F. biltmoreana* is hexaploid (NESOM 2010e). The latter two polyploids were not recognised by WALLANDER (2008) until NESOM (2010e) made a detailed study of the *F. americana* (White ash) complex. The polyploids are hypothesised to be derived from crosses between *F. americana* and *F. penn-*

sylvanica. All three species can be found in the vicinity of each other (NESOM 2010e) but they differ in morphology of the fruits, leaf and twig vestiture, and shape and thickness of petiole base (giving rise to different leaf scars).

Fraxinus profunda [Ill. 11b] is hexaploid (NESOM 2010a) and thought to be either a derivative of tetraploid *F. americana* (= *F. smallii*) and diploid *F. pennsylvanica* or autopolyploid of *F. pennsylvanica*.

Fraxinus pauciflora and *F. cubensis* were distinguished from *F. caroliniana* s.s. by NESOM (2010d). All three water ashes are similar in overall morphology and occur in swampy or riverine habitats.

Fraxinus americana and *F. pennsylvanica* [Ill. 13] are the two most common species of ash in USA. Many species are commercially important and especially the wood of *F. americana* which is used for making baseball bats. However, most species of ash in North America are now threatened by the Emerald ash borer (*Agrilus planipennis*), a beetle that is spreading fast across the eastern USA and has already killed tens of millions of ash trees (www.emeraldashborer.info). Huge efforts are being made to try to stop this disaster. Expeditions have been made to China in order to make collections of ash species there that could be used for breeding resistance genes into the American ashes (AIELLO 2012).



12 – *Fraxinus uhdei* is distributed and cultivated in tropical Americas. It has large leaves with petiolulate leaflets. Oaxaca, Mexico [E. Wallander, 12-02-2004]

SECTION *DIPETALAE*

This section contains three superficially not very similar species: *F. dipetala*, *F. quadrangulata* and *F. anomala*. But in the genus *Fraxinus*, they are unique in having quadrangular or four-angled twigs (due to development of corky ridges) and hermaphrodite flowers occurring in leafless lateral inflorescences. Other morphological similarities include oval to ovate shaped wings of the samaras,



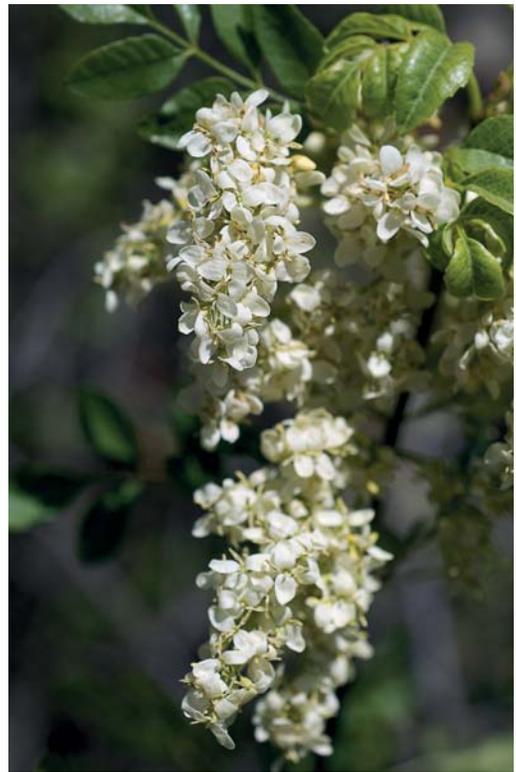
13 – (a) A staminate (male) inflorescence of *Fraxinus pennsylvanica* and (b) a detail of a male flower, consisting only of two stamens and a small calyx. Göteborg Botanical Garden, Sweden [E. Wallander, 28-04-2004]

contrasting to the more elongated wings characteristic of the samaras of the other sections. In other characters, such as petal number, leaf morphology, and growth habit, they are quite unlike each other.

Fraxinus dipetala (Two-petal ash) is a shrub or small tree restricted to dry areas of southwestern USA and northwestern Mexico. It is the only *Fraxinus* species having two petals, which are united and tubular by fusion with the filaments. Sometimes the petals are lacking and the two forms may occur in the same panicle. The flowers are fragrant and occur in many-flowered and showy inflorescences [Ill. 14]. The anthers are relatively large and protrude from the corolla, an indication that the flowers might be both wind- and insect-pollinated.

Fraxinus anomala (Single-leaf ash) is also a shrub or small tree, predominantly occurring in desert areas in southwestern USA and central Mexico. It is the only *Fraxinus* species where simple leaves [Ill. 15b] are the normal condition. There is a variety (var. *lowelli*) which has 3-5 leaflets [Ill. 15a]. *Fraxinus anomala* has bisexual or sometimes unisexual flowers with a persistent calyx, but lack corolla, and they appear in lateral panicles before or with

the young leaves [Ill. 15a]. They are apparently wind-pollinated.



14 – A sweet-scented inflorescence with two-petaled flowers of *Fraxinus dipetala*. California, USA
[“Eric in SF” Wikimedia Commons CC-BY-SA-3.0, 18-04-2009]



15 – (a) Flowering *Fraxinus anomala* var. *lowellii* with trifoliate leaves and (b) normal *F. anomala* with its unifoliate leaves. California, USA [Stan Shebs, Wikimedia Commons, 1-04-2007] & New Mexico, USA [R. Sivinski, June unknown year]

Fraxinus quadrangulata (called Blue ash because early European settlers in the USA made blue dye from the inner bark) is a large tree with conspicuously quadrangular twigs [Ill. 16], occurring in eastern and central North America. The flowers are mostly hermaphrodite, apetalous and wind-pollinated.

SECTION *ORNUS*

Within the genus *Fraxinus*, the 16 species of the section *Ornus* are unique in that the inflorescences are borne on current year shoots, together with the leaves, which emerge from terminal buds [Ill. 17]. In contrast, in all the other sections the inflorescences are borne laterally on previous year's shoots. There are two morphological groups in the section *Ornus*: the insect-pollinated species (or both wind- and insect-pollinated), with four white linear petals in each flower [Ill. 18b], and the wind-

pollinated, without petals. Both groups have calyx and the latter group has evolved from the former. There is a transition from hermaphrodite via androdioecious to dioecious species. Some of the insect-pollinated are androdioecious as well as some of the wind-pollinated species and dioecy has evolved after the evolution of wind-pollination [Ill. 1].

The 12 species with petalous flowers are *F. apertisquamifera*, *F. bungeana*, *F. floribunda*, *F. griffithii*, *F. hopeiensis*, *F. lanuginosa*, *F. malacophylla*, *F. ornus*, *F. paxiana*, *F. raibocarpa*, *F. sieboldiana* and *F. trifoliolata*. All are androdioecious except *F. griffithii*, *F. malacophylla* and *F. raibocarpa* which are hermaphrodite. The former has evolved from the latter. The four species with apetalous flowers are *F. baroniana*, *F. chinensis*, *F. longicuspis* and *F. micrantha*. The first two are dioecious and have evolved from the latter two, which are androdioecious.

The section *Ornus* contains most of the species with showy flowers and they are there-



16 – (a) The shoots of *Fraxinus quadrangulata* are four-ridged and in young shoots (b) this is very pronounced. Arboretum Wespelaar, Belgium [E. Wallander, 7-10-2012] & Von Gimborn Arboretum, The Netherlands [E. Wallander, 6-10-2012]



17 – The terminal buds of all species in the section *Ornus* contain the new shoot with both leaves and inflorescences. (a) The insect-pollinated *F. ornus* and (b) the wind-pollinated *F. longicuspis*. Göteborg Botanical Garden, Sweden. [E. Wallander, 23-05-1997] & Chichibu Mountains, Japan. [E. Wallander, 10-05-1999]



18 – *Fraxinus ornus* occurs in southern Europe and (a) the insect-pollinated flowers have a sweet scent. The species is androdioecious, meaning that trees have either (b) male or hermaphrodite flowers. Sicily, Italy [E. Wallander, 2-05-1996] & Göteborg Botanical Garden, Sweden [E. Wallander, 17-05-2000]

fore sometimes called the “flowering ashes”. A well-known and ornamental species of this kind is *F. ornus*, the Manna ash [Ill. 18], in the Mediterranean area. It is called so because it is or used to be cultivated, especially on Sicily, for its dried sap which is harvested through incisions in the bark to produce the sugar mannitol. Two other species with ornamental value are *F. floribunda* [Ill. 19a] (widespread from Afghanistan through Himalaya to Southeast Asia), and *F. paxiana* [Ill. 19b] (Himalaya and China). Especially the latter species has large and showy inflorescences.

Also *F. sieboldiana* (China, Japan and Korea) [Ill. 20a] and *F. lanuginosa* (Japan) [Ill. 20b] are ornamental. These two species are distinguished from each other by the former having entire margins of the leaflets and two pairs of inner bud scales and the latter having serrate margins and one pair of inner bud scales. Related to them are *F. apertisquamifera* (Japan) and the recently resurrected *F. hopeiensis* in northern China (LEE *et al.* 2012).

Fraxinus griffithii is one of the two ever-green ashes. It occurs in tropical southeastern Asia [Ill. 21]. The shoot has no winter buds and a more or less continuous growth. The flowers are fragrant, hermaphrodite and insect-pollinated.

Fraxinus chinensis is a complex of taxa with uncertain status and there may be polyploidy involved. Two subspecies are accepted: *F. chinensis* subsp. *chinensis* and *F. chinensis* subsp. *rhynchophylla* (including *F. rhynchophylla* and *F. japonica*). The former has a more southern distribution in Asia (China, Korea, Vietnam and Thailand) and the latter more northern (China, Korea, Japan and southeastern Russia).

Fraxinus chinensis [Ill. 22a] belongs to the wind-pollinated group and the flowers are apetalous and unisexual. The Japanese *F. longispis* [Ill. 17b & 22b] is also wind-pollinated but androdioecious (at least morphologically so) (WALLANDER 2001). In the Himalayas occurs the similar *F. micrantha*.

Fraxinus baroniana is relatively unknown but has very attractive foliage with long narrow leaflets with beautiful autumn colour [Ill. 23]. It is a rare, small tree and occurs on slopes and along rivers and streams in central China (Sichuan, Gansu and Shaanxi). Seeds of this species have been collected and spread to researchers and arboreta (AIELLO 2012). A DNA analysis (WALLANDER, unpublished data) of this accession showed that it is related to *F. chinensis* and the other apetalous species in the section *Ornus*.



19 – (a) Flowering *Fraxinus floribunda* and (b) fruiting *F. paxiana*. Arboretum Wespelaar, Belgium [Ph. de Spoelberch, 16-05-2006] & north Yunnan, China [Ph. de Spoelberch, 5-07-2008]



20 – (a) Hermaphrodite *Fraxinus sieboldiana* (with an enlarged male flower from another tree) and (b) *F. lanuginosa*. Chichibu Mountains, Japan [E. Wallander, 8-05-1999] & Göteborg Botanical Garden, Sweden [E. Wallander, 16-05-2000]



21 – *Fraxinus griffithii*, occurring in tropical Asia, is evergreen. (a) The shoots have no winter buds and a more or less continuous growth. (b) The flowers are fragrant, hermaphrodite and insect-pollinated. Arboretum Wespelaar, Belgium [E. Wallander, 7-10-2012] & Kyoto University Garden, Japan [S. Nanami, 11-07-1999]



22 – (a) Male *Fraxinus chinensis* and (b) hermaphrodite *F. longicuspis*. The flowers are wind-pollinated and borne in lax inflorescences which emerge at the same time as the leaves, but flower while the leaves are still small and not so much in the way for pollen dispersal. Göteborg Botanical Garden, Sweden [E. Wallander, 13-05-2000] & Chichibu Mountains, Japan [E. Wallander, 5-05-1999]



23 – The rare *Fraxinus baroniana* in autumn colours. Jia Ling River, Gansu Province, China [Kunso Kim, 6-10-2011]

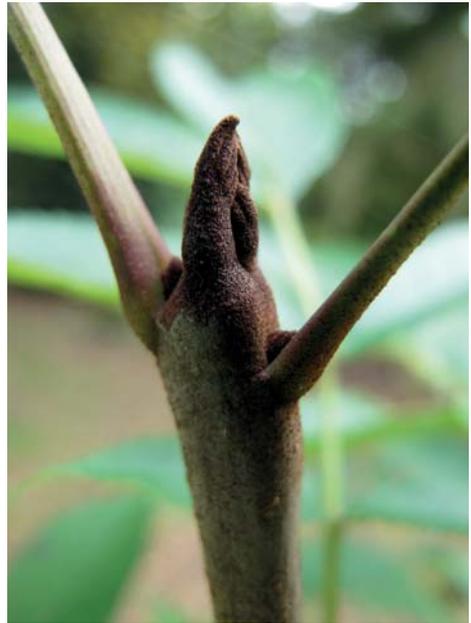
INCERTAE SEDIS

Three species are still unplaced in the present classification. The American species *F. cuspidata* [Ill. 24] is a small insect-pollinated tree occurring in Mexico and southwestern USA. Although having four petals, its flowers are not similar to those of the insect-pollinated species in the section *Ornus*. The petals are united and form a tube about one third of the length of the corolla, not free as in the section *Ornus*. The two stamens are united with the corolla tube and shorter than the petals. The fragrant and hermaphrodite flowers are borne terminally in lateral, leafy panicles developed from the axils of the leaves of the previous year, not in terminal panicles on current year shoots as in the section *Ornus*. *Fraxinus cuspidata* is more similar to *F. dipetala*. The latter also has a sympetalous corolla fused with the filaments but with two instead of four petals. They both have inflorescences on lateral shoots but they are not leafy in *F. dipetala*. However, molecular data (several different loci) show that they are not closely related (WALLANDER 2008).

Fraxinus chiisanensis is endemic to Korea and has some primitive characters such as the naked terminal bud [Ill. 25]. It is a wind-pollinated tree with lateral inflorescences on the shoot of previous year. The bisexual or unisexual flowers are apetalous and with a calyx



24 – *Fraxinus cuspidata* is a small tree with fragrant flowers in arid areas of southwestern USA and Mexico. Sacramento Mountains, New Mexico, USA [R. Sivinski 28-04-2005]



25 – *Fraxinus chiisanensis* from Korea with its characteristically naked bud. Arboretum Wespelaar, Belgium [E. Wallander, 7-10-2012]

which is persistent on the samaras. In most of its morphological characters, and also leaf flavonoids (MIN *et al.* 2001, CHANG *et al.* 2002), it resembles the *Melioides*, but the molecular data (WALLANDER 2008) does not place it in that section.

Fraxinus platypoda is a large wind-pollinated tree, occurring in China and Japan. It has lateral inflorescences with polygamous and apetalous flowers. Calyx is present only in pistillate flowers and persistent on the samaras, which have a flattened seed cavity. The species has characteristically swollen petiole bases covering the lateral buds [Ill. 26]. Previous molecular work (WALLANDER 2008) suggested that *F. platypoda* in China was closely related to *F. mandshurica* and that *F. spaethiana* (Japan) was a separate species, but a recent re-analysis (WALLANDER, unpublished data) showed that they should be treated as the same species (as done by NAKAIKE 1972 and WEI & GREEN 1996). The name *F. platypoda* has nomenclatural priority over *F. spaethiana*. The flavonoid study by MIN *et al.* (2001) was inconclusive about the sectional affiliation and unfortunately the most recent molecular analysis (WALLANDER, unpublished data) did not shed more light on the position.



26 – *Fraxinus platypoda* with characteristically swollen leaf petioles protecting the next year's floral buds. Arboretum Wespelaar, Belgium [Ph. de Spoelberch, 22-05-2012]

ACKNOWLEDGEMENTS

I thank Dr. Piet de Jong of the Dutch Dendrology Society and Philippe de Spoelberch, president of the Belgian Dendrology Society, for inviting me to the study days of *Fraxinus* in the two societies. I also thank Philippe de Spoelberch for allowing me to make collections of *Fraxinus* in the Arboretum Wespelaar and Dr. Koen Camelbeke for sending me additional samples. I am indebted to Dr. Johan Rova, Göteborg University, Sweden, for doing the DNA analysis of the collected samples.

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