The Ulmaceae of the World

Nicolas Küffer – Yann Fragnière – Yi-Gang Song – Gregor Kozlowski



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Ulmus minor (gk)

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CONTENTS

7 Foreword

8 The Ulmaceae: An overview

12 The genera of Ulmaceae
14 *Ampelocera*
16 *Phyllostylon*
18 *Holoptelea*
20 *Hemiptelea*
22 *Planera*
24 *Ulmus*
26 *Zelkova*







28 The Ulmaceae people

41 Acknowledgements

42 Selected references



A mixed forest of *Quercus coccifera, Acer sempervirens* and *Zelkova abelicea* in the Dikti Mountains in Crete, Greece (lf)



Foreword

Dr Koen Camelbeke
Chairman of the Expert Committee
Fondation Franklinia

Botanical nomenclature rules require that a plant family be named after one of its genera. In the case of Ulmaceae, this distinction naturally highlights the genus *Ulmus*. Elm trees have regained popularity and are highly valued today, largely due to the development of disease-resistant varieties capable of withstanding Dutch elm disease. Although elms suffered severe losses in the last century, they are now widely planted again in streets, parks, and landscape settings. In European arboreta, too, they are receiving renewed attention, alongside the well-loved genus *Zelkova* – with *Zelkova serrata* as the clear favourite – and the unusual monotypic *Hemiptelea davidii*, notable for its striking thorns.

This publication is the culmination of the Project *Zelkova* at the Botanical Garden of the University of Fribourg, Switzerland. In many ways, this booklet represents the crowning achievement of years of research and conservation efforts on the Ulmaceae family by Prof. Kozlowski and his team, who have focused, among other subjects, on *Zelkova abelicea* in Crete and *Zelkova sicula* in Sicily.

This booklet is truly unique. It is likely the first time that all seven genera of Ulmaceae have been brought together in a single publication and illustrated so beautifully with high-quality images. Even the little-known (sub)tropical species, some bearing nearly unpronounceable names, are included.

The authors deserve congratulations for compiling this wealth of information in such a concise, attractive, and user-friendly format. I am confident that this work will further enhance the reputation and appreciation of this remarkably beautiful and fascinating plant family.

The Ulmaceae: An overview

Introduction
Although among the smaller plant families in terms of species richness, Ulmaceae holds disproportionate scientific, ecological, economic, and cultural significance. Its members are exclusively woody – primarily deciduous, and more rarely evergreen trees and shrubs – distributed largely across the Northern Hemisphere, with additional representation in tropical regions. Despite its limited diversity, the family provides an important model for research in paleobotany, historical biogeography, systematics, plant evolution, and diversification processes.

Beyond its scientific interest, Ulmaceae includes species that have profoundly shaped human societies. For centuries, elms and their relatives have influenced landscapes, supplied durable and valuable timber, and played a significant role in cultural traditions as well as in the development of urban environments.

Nevertheless, the family remains incompletely studied. While temperate taxa have long attracted the attention of botanists and foresters, many tropical representatives are still poorly documented. Fundamental aspects of their ecology, reproductive biology, geographic distribution, and phylogenetic relationships remain insufficiently understood.

An ancient lineage
Ulmaceae represents an evolutionarily ancient lineage, with a fossil record extending back to the early Cenozoic. By the early Paleocene, members of the family were already widely distributed across the Northern Hemisphere. The earliest confirmed fossils of extant genera such as *Ulmus* and *Zelkova* date to the Eocene. Fossil leaves and fruits attributable to *Ulmus*, for example, have been documented from early Eocene deposits in China (approximately 50 million years ago) as well as from middle- to late-Eocene strata in North America.

Paleobotanical evidence further suggests that the family's historical diversity exceeded its present-day composition. Several genera that were once widespread are now extinct. One notable example is *Cedrelospermum*, known from Paleogene and Neogene deposits across Europe, Asia, and North America before its eventual disappearance for reasons that remain unclear. Other genera have persisted only as geographically restricted relicts. *Zelkova*, for instance, now exhibits a strikingly disjunct distribution between eastern Asia and southwestern Eurasia. Such patterns underscore the relictual nature of many Ulmaceae lineages and highlight their importance as indicators for reconstructing past vegetation dynamics and paleoclimatic conditions.


1

1. In a beautiful landscape near Lerik (Azerbaijan) grows *Zelkova carpinifolia*. (gk)

2. *Trema micranthum*, a species now classified in the Cannabaceae (formerly included in a broader concept of the Ulmaceae), occurs in the Caribbean and Mesoamerica and bears fleshy fruits. (inat-miamiwitch)

3. A branch of *Ulmus minor* from Switzerland showing its typical fruits. (gk)

4. Fleshy fruits are characteristic of the genus *Ampelocera*, as illustrated here by *Ampelocera ruizii* from the western Amazon Basin. (aam)

5. Most members of the Ulmaceae produce winged fruits known as samaras. This relatively large samara belongs to *Holoptelea integrifolia* from India. (ab)

6. Within the genus *Zelkova*, only *Zelkova sinica* produces such hemispherical fruits. (ys)





A complex systematic history

The taxonomic circumscription of the Ulmaceae has undergone substantial revision over time. When the family was first formally described in 1815, it comprised only two genera, *Ulmus* and *Celtis*. For nearly a century and a half, classifications divided the group into two principal subfamilies reflecting these lineages – Ulmoideae and Celtidoideae – often informally referred to as the "ulmoids" and "celtoids."

This framework began to change with the advent of molecular phylogenetics in the late twentieth century. Genetic evidence demonstrated that the celtoid lineage is more closely related to members of the Cannabaceae than to Ulmaceae. As a result, these taxa were reclassified, and modern phylogenetic studies now define Ulmaceae more narrowly. Within this revised circumscription, two principal clades are recognized: a temperate lineage and a tropical lineage.

The temperate clade includes the genera *Ulmus, Zelkova, Planera*, and *Hemiptelea*, whereas the tropical clade comprises *Ampelocera, Phyllostylon*, and *Holoptelea*.

Floral diversity, fruits, and dispersal

The reproductive biology of the Ulmaceae exhibits notable diversity. Some genera, including *Zelkova* and *Planera*, may produce three floral morphs – staminate (male), pistillate (female), and hermaphroditic – occasionally even on the same branch. Such variation reflects complex breeding systems that can enhance reproductive flexibility under variable environmental conditions.

Flowers are typically small and inconspicuous, consistent with predominantly wind-mediated pollination. As in other urticalean rosids, they possess a single perianth whorl composed of four to eight green or brown tepals. The number of stamens generally corresponds to the number of tepals, though exceptions occur: *Holoptelea* may produce up to twelve stamens and *Ampelocera* up to sixteen. The ovary is superior and bicarpellate, terminating in two slender styles. Fruit morphology and dispersal strategies are remarkably varied. *Zelkova* produces asymmetric, unwinged fruits resembling achenes, often interpreted as representing a relatively primitive condition within the family. In contrast, *Ulmus, Hemiptelea, Holoptelea,* and *Phyllostylon* bear winged fruits adapted primarily for anemochory (wind dispersal). The fruits of *Hemiptelea* are particularly distinctive, possessing a unilateral wing that may represent an intermediate stage in the evolution of wind-dispersed diaspores.

Other dispersal mechanisms also occur. The fruits of *Planera* exhibit fleshy protuberances and are likely dispersed by water, reflecting the species' riparian habitat. In the neotropical genus *Ampelocera*, large, often brightly colored drupes suggest dispersal by birds. An unusual mechanism occurs in *Zelkova*, where small twigs bearing clusters of fruits and dried leaves detach from the tree. The persistent leaves increase drag, enabling the entire unit to disperse by wind or gravity.







Diversity, biogeography, and human connections

Current classifications divide the family into two major clades. The temperate clade includes four genera – *Ulmus, Zelkova, Planera*, and *Hemiptelea* – with about 43 species, while the tropical clade comprises three genera – *Ampelocera, Phyllostylon*, and *Holoptelea* – containing roughly 13 species.

Scientific attention has been unevenly distributed. Temperate taxa, particularly *Ulmus*, have been extensively studied due to their economic and cultural significance. In contrast, tropical representatives remain comparatively understudied, and even fundamental data concerning their ecology, distribution, and conservation status are often incomplete.

Human societies have long maintained close relationships with members of the family. Various species of *Ulmus* historically dominated rural and urban landscapes across Europe, Asia, and North America, valued for their durable timber, shade, and ornamental qualities. In eastern Asia, *Zelkova serrata* – the keaki tree – has similarly been prized in traditional architecture, forestry, and urban planting. Tropical members also possess local significance: species of *Phyllostylon* provide wood for tools and construction, while *Holoptelea* species are used in traditional medicine and may have pharmacological potential. These associations highlight the need for continued research and sustainable management.


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Leaf diversity in the elm family (Ulmaceae):

1. *Phyllostylon rhamnoides* from Central and South America. (fsc)

2. *Ulmus glaucescens* from eastern China. (inat-wresy)

3. *Ulmus glabra* probably the most widespread species in the family. (gk)

4. *Ulmus laciniata* found in China, Russia, Korea and Japan. (inat-biflab)

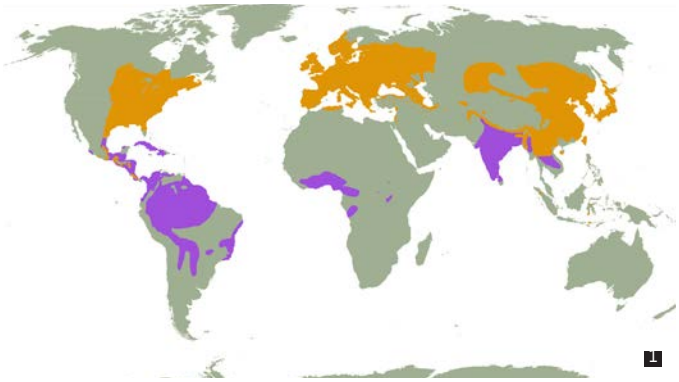
5. *Hemiptelea davidii* from China and the Korean Peninsula. (ys)

Biogeographical patterns

The global distribution of Ulmaceae reveals several notable patterns. Contrary to the common perception that it is primarily temperate, a substantial portion of its diversity occurs in subtropical and tropical regions. Roughly one quarter of all species belong to the tropical clade. In addition, several temperate species extend into tropical areas, and one species of the temperate clade, *Ulmus lanceifolia*, even reaches the Southern Hemisphere, occurring as far south as the Indonesian islands of Sulawesi and Flores.

Interestingly, the elm family does not follow to the typical latitudinal diversity gradient in which species richness peaks near the equator. Instead, the highest diversity occurs in the subtropical belt roughly between 28° and 38° north latitude. Similar patterns are seen in other small woody families with many relict taxa, such as Juglandaceae.

The main center of diversity is southeastern Asia, particularly China, with secondary centers in the southeastern United States and in Mesoamerica and northern South America.



1



2

1. Global distribution of the elm family. In orange the temperate clade (*Ulmus, Zelkova, Planera* and *Hemiptelea*); in purple the tropical clade (*Ampelocera, Phyllostylon* and *Holoptelea*). (yf)

2. An insufficiently studied species is *Holoptelea grandis*, found in the tropical forests of western Africa. (inat-peterneuenschwander)

3. In threatend remnants of seasonally dry forests in central Colombia, a new species of *Ampelocera* has been described as *A. percyhernandezii*. (bvt)

4. Subtropical forests of Jeju Island in South Korea support dense stands of *Zelkova serrata*. (gk)



3



4

Purpose of this book

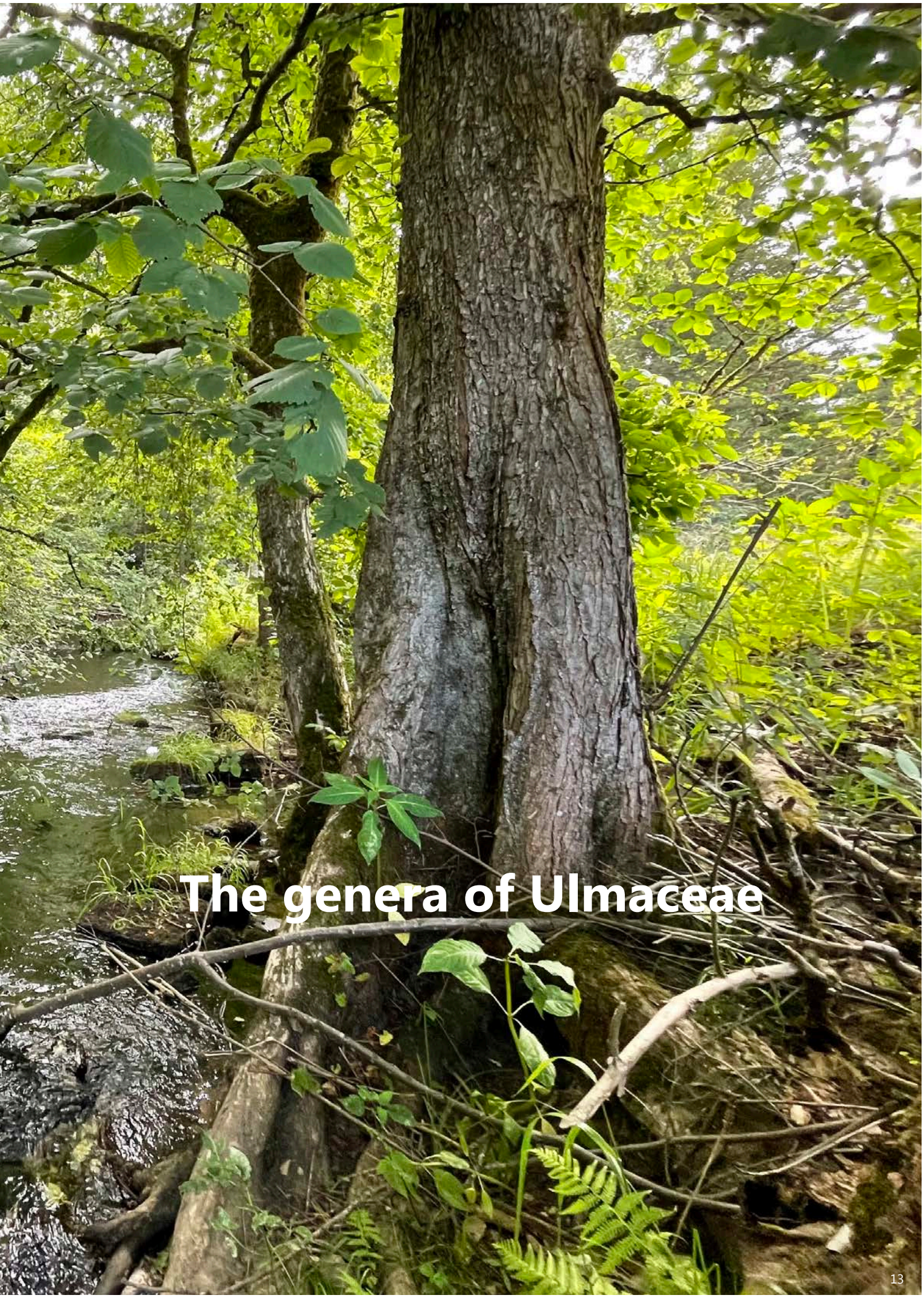
This booklet was conceived with three principal aims. First, it presents all genera of Ulmaceae in a richly illustrated format, offering a visual overview of its diversity. Such a comprehensive illustrated synthesis has not previously been produced and is largely based on the global analysis of Fragnière et al. (2021).

Second, it highlights key individuals involved in the study, exploration, and conservation of Ulmaceae, as well as those inspired by these remarkable trees.

Finally, this publication represents the culmination of two long-term initiatives dedicated to their understanding and preservation: Project *Zelkova* and Project *Ulmus laevis*. In this sense, the booklet serves both as a milestone of these efforts and as an invitation for further research, exploration, and conservation of the elm family.



Ulmus laevis in its natural habitat near Eberbach in the Odenwald region, Germany (gk)



The genera of Ulmaceae

Ampelocera Klotzsch

11 species



Age and origin
The origins of this neotropical genus remain only poorly understood.

Extant species
The 10–11 species in this genus grow in the tropical rainforest of the Americas: *A. albertiae, A. cubensis, A. edentula, A. glabra, A. hottlei, A. longissima, A. macphersonii, A. macrocarpa, A. ruizii, A. verrucosa*. In 2024 a new species, *A. percyhernandezii*, was described from seasonally dry forests in central Colombia.

Habit
Ampelocera is characterized by its large tree habit (up to 30 m), sometimes with narrow buttressed trunks. The leaves typically have oblique bases and entire margins. Its inconspicuous cream-colored or yellowish-green flowers are arranged in dichasia with 4 to 16 stamens and a bifid style. Bisexual flowers usually occur in the upper part of the inflorescence, while lower portions only bare male flowers.
The size and shape of the drupaceous fruits are diagnotic at species level: glabrous (*A. glabra, A. longissima*), sparsely puberulent (*A. edentula, A. macrocarpa, A. percyhernandezii*), pubescent (*A. macphersonii*) or densely pilose (*A. ruizii*). Some species show additional distinctive traits, such as asymmetrical fruits (*A. hottlei*) or an exceptionally thick endocarp (*A. macrocarpa*). Flowering phenology varies among species: from August to November on leafless branches (*A. glabra, A. cubensis*), throughout the year (*A. edentula*), or mainly in spring (*A. hottlei, A. longissima, A. macrocarpa*).

Ecology
All species grow in tropical or subtropical rainforest at low to mid elevations, mostly below 700 m a.s.l. Some of them seem to be restricted to undisturbed primary tropical rainforest.

Distribution
Ampelocera species grow from southern Mexico trough Mesoamerica and South America till Bolivia and the Mata Atlântica at the Atlantic coast of Brazil. Roughly from north to south the species are distributed as follows: *A. hottlei, A. macrocarpa, A. macphersonii, A. percyhernandezii, A. albertiae, A. longissima, A. edentula, A. ruizii, A. verrucosa, A. glabra*. One species, *A. cubensis*, is restricted to Cuba and Hispaniola of the Greater Antilles in the Caribbean.


1


2

1. The pubescent fruits are characteristic for *A. macphersonii*. (inat-juanfcruzm)


3

2. and 4. This *A. hottlei* with buttress roots grows in central Belize. Its fruits are slightly asymmetrical. (inat-jmeerman)


4

3., 5. and 6. These exceptionnally large fruits belong to *A. macrocarpa*, as the name suggests. The flowers have tiny (1-2.5 mm) greenish sepals, the filaments reach up to 2 cm in length, with 1 mm long anthers, and are arranged in compound dichasia with bisexual flowers towards the apex and staminate flowers at the base. (nz, inat-marvinlopez, nz)


5


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7. Known only from primary rainforests of the upper Amazon Basin, *A. longissima* shows the typical drip tip common among many tropical rainforest trees. (Field Museum of Natural History, Chicago)



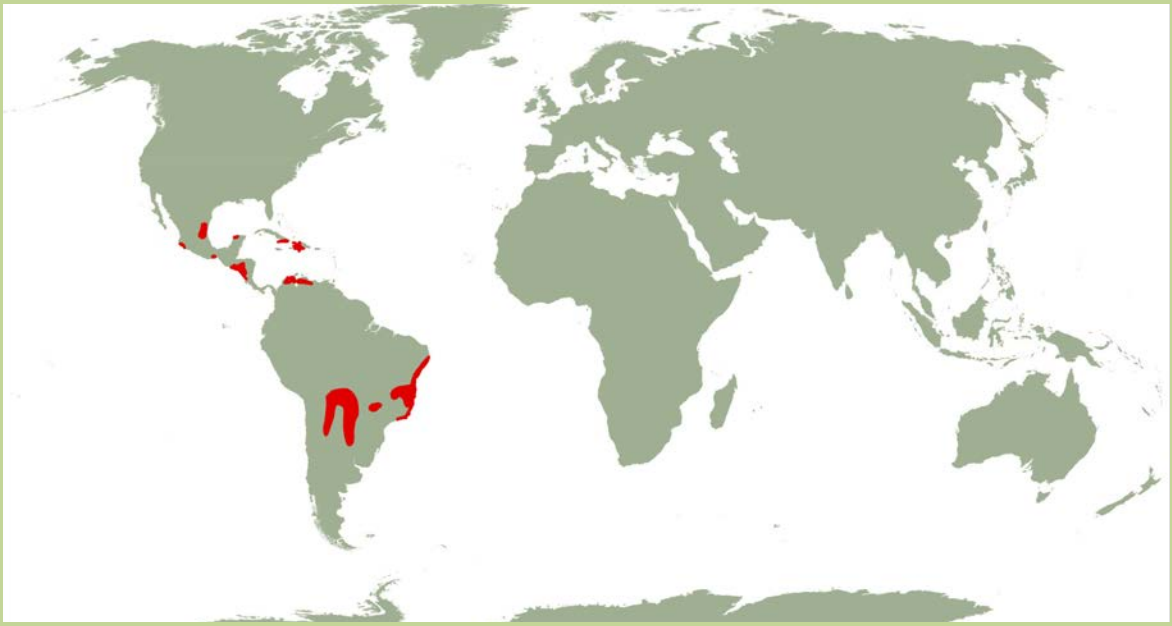
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8

8. *Ampelocera albertiae* is endemic to Colombia and grows in dense natural forests. (inat-thalia-mite)

Phyllostylon Capan. ex Benth. & Hook. f.

2 species



Age and origin

Little is known about the origins of the tropical clade within the Ulmaceae (genera *Ampelocera*, *Phyllostylon* and *Holoptelea*). Molecular analyses suggest that this clade originated around 44 million years ago, however, no definitive fossil record has yet been documented.

Extant species

Two species are accepted in the genus: *Ph. brasiliense* and *Ph. rhamnoides*.

Habit

Small to medium-sized trees with a typically slender, narrow crown. They may grow up to 24 m in height, but rarely exceed 15 m. Characteristic is also the channeled trunk and, at the base, the buttress roots. Leaves are alternate, small and elliptic, 2–5 x 1–3 cm, with a sharp tip. The margins are often unregularly serrate in the apical half. Flowers are bisexual or unisexual, occuring on the same tree, small (3–5 mm in diameter) and composed of 5–7 free tepals. The fruit is a winged samara with two unequally marked wings, the larger being up to five times the size of the smaller one.
Flowering occurs between September and November, with fruits ripening from October to December.

Ecology

Phyllostylon rhamnoides grows in scrub forests, often on calcareous or rocky, brushy soils in Central America. In South America it occupies a broader ecological range: from moist and semi-moist forests to rather dry or seasonally dry habitats as the Chaco or inter-Andean forests.
Restricted to the Mata Atlântica of Brazil, *Ph. brasiliense* occurs exclusively in the humid, dense tropical rainforest on the Atlantic coast of southeastern Brazil.

Distribution

The two species have distinct distribution ranges: *Ph. rhamnoides* occurs in Central America, the Carribbean and the southern Amazon basin, whereas *Ph. brasiliense* is restricted to the Atlantic rainforest of Brazil.



1. The pronounced asymmetry of the winged fruits is clearly visible in the central part of the photograph. (inat-tereso30)

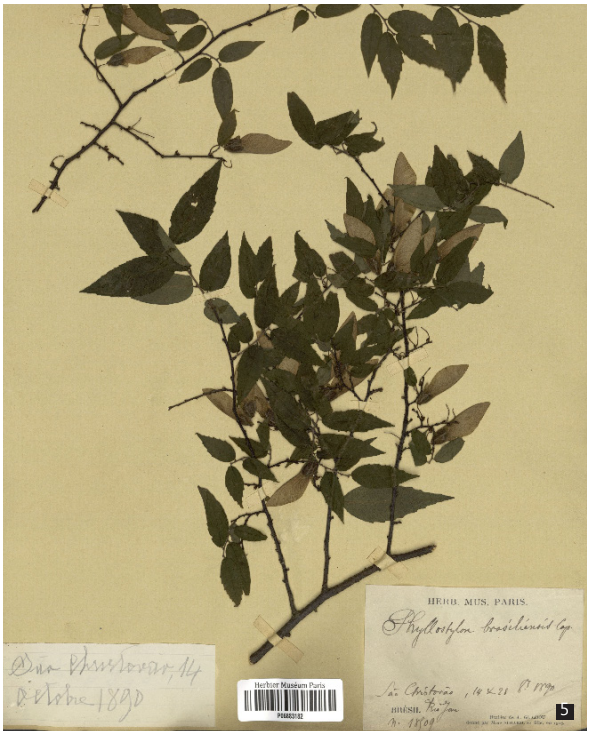




2. and 3. The leaves are irregularly serrate, especially in the apical half. (inat-andrey100; inat-mreith)



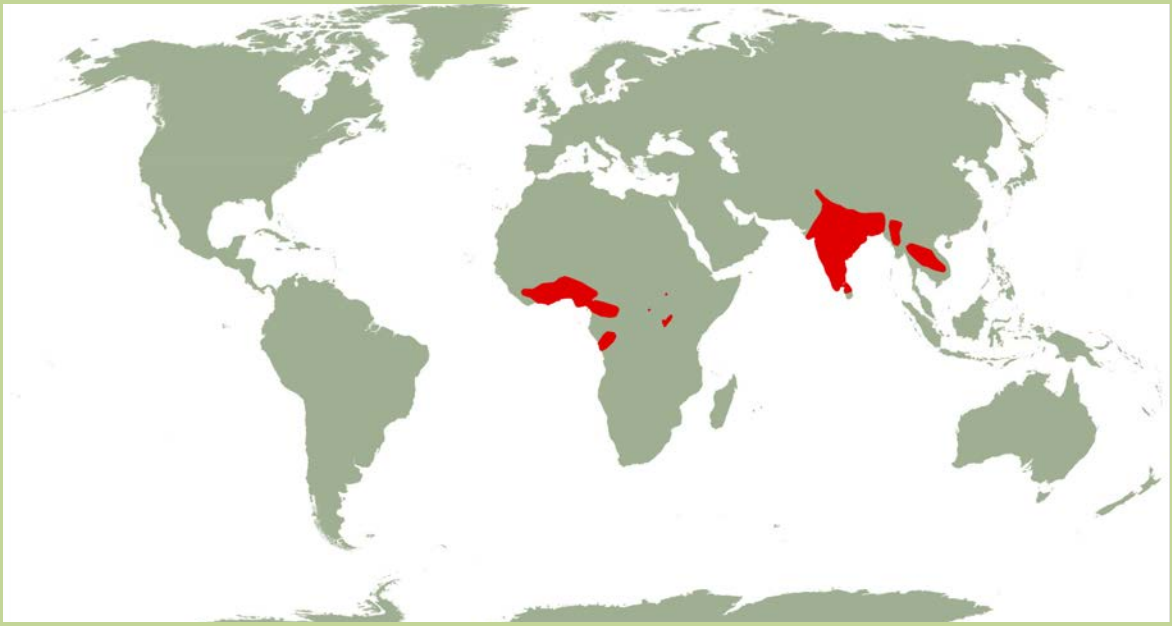
4. Buttress roots are characteristic of the stem of *Ph. rhamnoides*. (arbolesdelchaco.com)



5. Herbaria often preserve valuable information on historical species distributions, as in the case of *Ph. brasiliense* from São Cristóvão, now a densely populated neighboorhood within the bondaries of Rio de Janeiro. (Herbier Muséum Paris)

Holoptelea Planch.

2 species



Age and origin

Little is known about the fossil record of the tropical clade within the Ulmaceae (genus *Ampelocera*, *Phyllystylon* and *Holoptelea*), as is the case for many predominantly tropical groups.

Extant species

The genus includes two extant species: *H. grandis* from tropical Africa and *H. integrifolia* from India and Indochina.

Habit

The deciduous trees can reach up to 50 m in height, however *H. integrifolia* rarely exceeds 30 m. The bark is greyish and rough; it peels in older trees. The alternately arranged leaves are somewhat smooth and show entire or, more rarely, toothed margins. They are elliptic in shape, measuring 8-13 cm in length and 4-6 cm in width. When crushed, the leaves emit an unpleasant odour. The greenish to brownish flowers are tiny, with 4-6 tepals only 1-2 mm long. *Holoptelea grandis* typically flowers in January, with fruits maturing in February–March, when twigs are leafless.

In both species, the fruits resemble those of true elms: they are circular and winged on both sides, but generally much larger than in the genus *Ulmus*: up to 2.5 cm (*H. integrifolia*) or even up to 4.5 cm (*H. grandis*). *Holoptelea grandis* is otherwise very similar, though it has slightly larger leaves (5–18 cm long and 3–9.5 cm wide) and tendence to develop large, angular buttresses.

Ecology

Holoptelea grandis occurs in the tropical biome of sub-Saharan Africa, where it grows in rainforests as well as in drier semi-deciduous and riverine forests, often along watercourses from 230-1200 m a.s.l.

Holoptelea integrifolia is found in lowland areas but also occurs in forests up to 1100 m a.s.l. The species is easily propagated and cultivated. Its rather fast growth makes it a frequent choice for planting in parks and gardens.

Both species are pioneer species and therefore produce large numbers of fruits. Seedlings and young trees are often found in canopy gaps and on abandoned land. Natural regeneration occurs readily. Germination rates also appear to be high.

Distribution

The African species *H. grandis* occurs from Guinea and Liberia in the west to the great lakes region of East African, forming a broad belt across the continent. To the north and south of its ranges, it seems to be too dry at least seasonally.

The Asian species *H. integrifolia* is found mainly in India, but its distribution extends further east and south to Vietnam and the Malay Peninsula.





1. *Holoptelea integrifolia* flowers in February in southern India, before the leaves emerge. (inat-treecloudspermaculture)

2. The leaves of *H. integrifolia* have an entire margin, as the name suggests. (inat-drcf-chaudhari)



3. The wind dispersed fruits, with their broad, more or less symmetrical wings, reach up to 2.5 cm in diameter in *H. integrifolia*. This enables the species to colonize new habitats rapidly and efficiently. (inat-rujutavinod)

4. *Holoptelea grandis* from tropical western Africa colonizes a wide range of habitats, from dense rainforests to drier semi-deciduous forests. (inat-peterneuenschwander)





5. The bark of *H. integrifolia* is rather rough and tends to exfoliate in older, mature specimens. (inat-ravaljay)



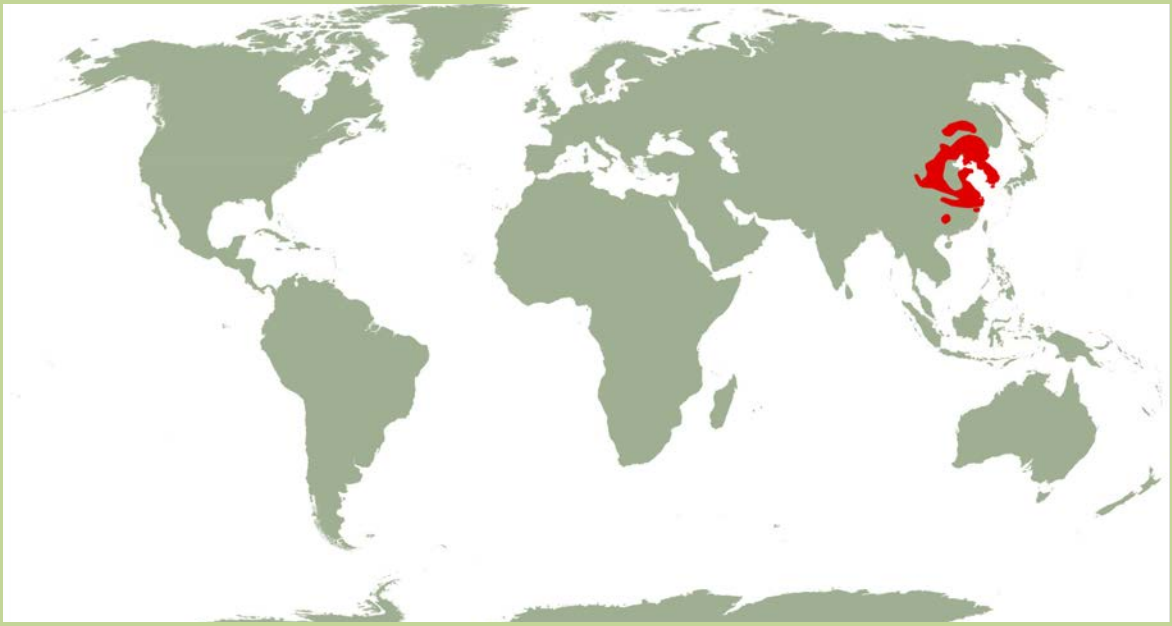
6. Typically, the seed of *H. integrifolia* is located in the apical part of the winged fruit. (inat-deepthitas)



7. A fruiting specimen of *H. integrifolia* from western India. Photograph taken in mid-March. (inat-kpakilan2012)

Hemiptelea Planch.

1 species



Age and origin
In Europe, fossils of the genus are documented from mid-Oligocene to Pliocene deposits. In Japan, the fossil record extends into the latest glacial sediments. Biologists even described a species (*H. mikii*) from Pleistocene deposits in southern Japan, where the genus is now extinct. It is curretly unknown from the fossil record of the Americas.

Extant species
Hemiptelea is a monotypic genus. *H. davidii* is native to East Asia.

Habit
This small deciduous tree species reaches heights of up to 10 m. The bark is grayish-brown and deeply grooved. The twigs are greyish and bare spines 2–10 cm long. The mostly elliptic leaves are borne on a short (3–5 mm), pubescent petiole and have margins with characteristic obtuse teeth. Flowers appear together with the leaves in April-May and are arranged in groups of 2–4 in the leaf axils. The tiny flowers have 4–5 petals and are mostly bisexual, though sometimes functionally male. The fruits are yellowish-green, ovoid and asymmetric, with a wing only on one side, measuring 5–7 mm in length. They ripen in September and October.

Ecology
Grows in loose forests and shrublands below 2000 m a.s.l. on hill slopes and trail slides in moderately moist places.

Distribution
Hemiptelea davidii grows in China and on the Korean Peninsula from Manchuria in the north till central China.



1. and 2. The English name “thorn elm” gets immediately apparent when observing the spines on the branches. The leaves are rather variable in size, ranging from 4–7 cm in length. (flickr-helicongus, inat-liboheng_reborn)



3. The flowers appear in spring at the same time as the leaves. (ek)



4. *Hemiptelea davidii* is an often planted in parks and arboreta, as here in Denmark. (ek)

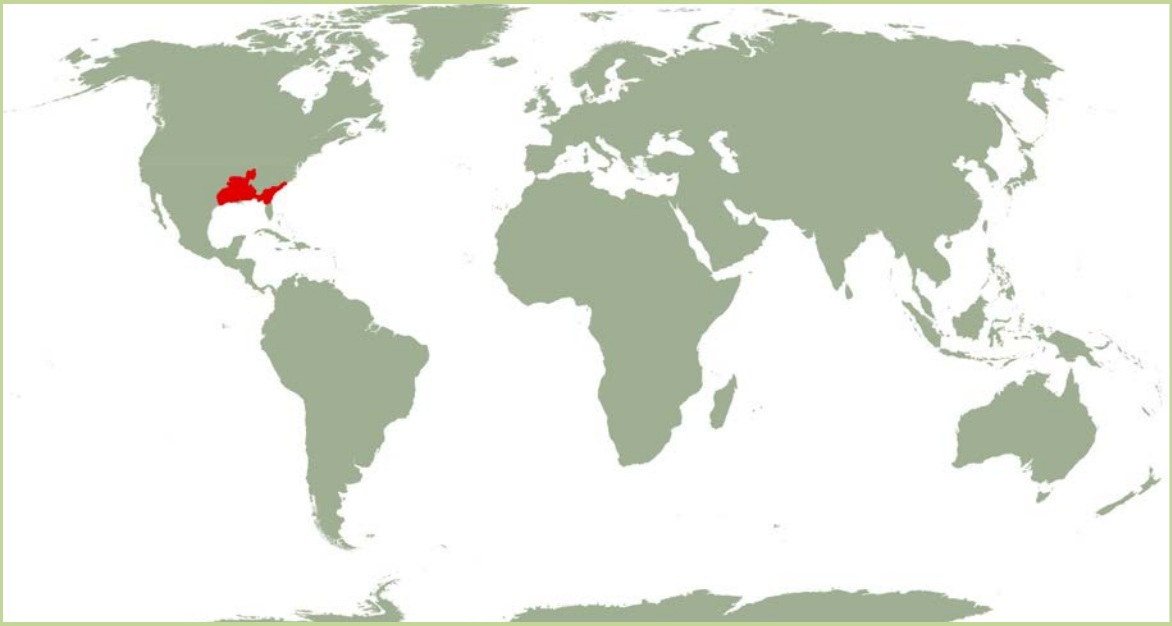


5. The small greenish fruits are ovoid and somewhat thin. They ripen in autumn. (Nemzetközi Dendrológia Alapítvány dendrologia.eu)



Planera J.F. Gmel.

1 species



Age and origin
The oldest fossils of the genus known so far have been found in North America and date from the early Eocene. Fossils have also been discovered in present-day Siberia and Europe, dating to the middle Eocene.

Extant species
The genus is monotypic, containing only one extant species: *P. aquatica*.

Habit
Small, deciduous trees reaching up to 15 m in height. The bark is grayish brown and develps loose, flaky scales, a distinctive character for *Planera* not seen in the other genera of Ulmaceae. Leaves alternate, with drop-shaped blades 3–7 cm long, serrate margins and a pubescent underneath. The flowers are tiny and greenish-brown. In contrast to the true elms (genus *Ulmus*), the genus *Planera* does not produce winged samaras, but small brown drupes, 1–1.5 cm in diameter.

Ecology
It grows along rivers and streams in seasonally or temporally flooded habitats, as well as in swamps or along lakes shores, mostly at low elevations.

Distribution
Planera aquatica only grows in the United States of America ranging from eastern Texas to North Carolina and extending northward along the Mississippi River valley to southern Illinois.







1. One of the approximately 20 fossil species of *Planera*: *Planera nervosa* from the Green River Formation in Utah, USA. (fossilera.com)

2. The sessile flowers are very small, with curled, hairy stigmas and appear with the leaves in early spring. (inat-cjs041)

3. The fruits are soft, prickly nuts, 10–15 mm in diameter, rather than winged seeds typical of true elms. (inat-pbarbour_1978)





4. and 5. The ovate to elongate leaves typically have serrate margins. They are dark green on the upper surface and paler beneath. (inat-jrichardabbott)

6. The bark is scaly, shreddy and patchy, with a grayish-brown outer surface and a more reddish colour where it exfoliates in patches. (inat-jeffwilson2)

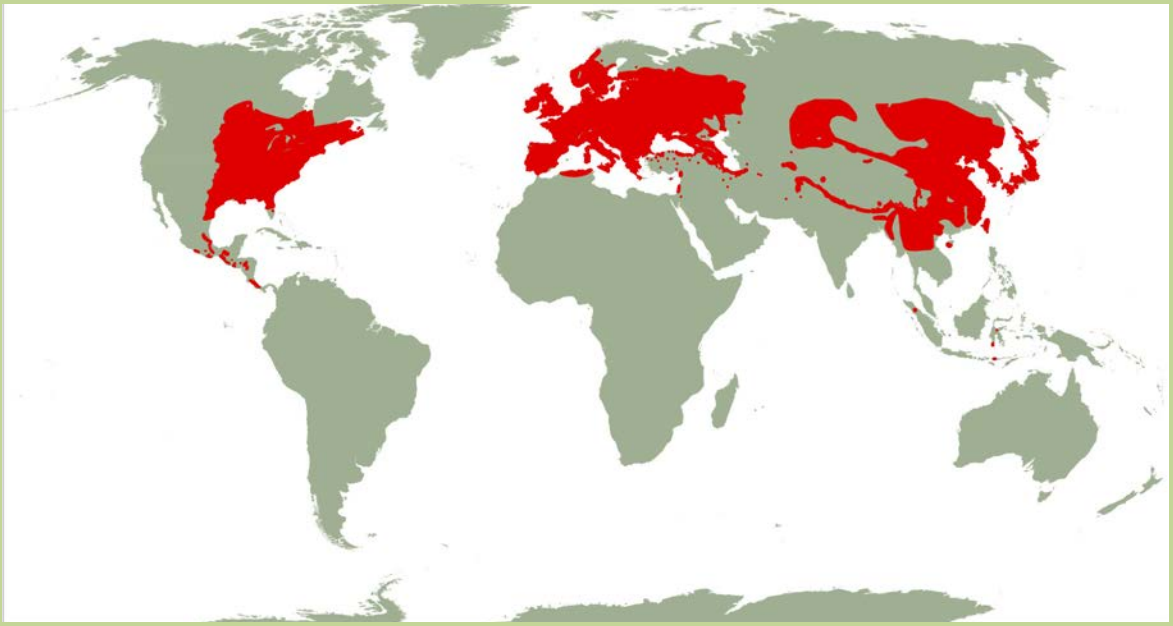




7. Typical habitat of the water elm in the southeastern United States, consisting of seasonally flooded forests. (inat-jakes26)

Ulmus L.

37 species



Age and origin
The oldest fruit fossils date back to the late Early Eocene of western North America. Extensive leaf and fruit fossil records are also known from Central and East Asia, attributed to sections *Microptelea* and *Ulmus*, with the earliest records dating to the Paleocene.

Extant species
This is by far the largest genus of the Ulmaceae with approximately 37 species. Eurasia accounts 29 species: *U. bergmanniana, U. boissieri, U. castaneifolia, U. changii, U. chenmoui, U. chumila, U. davidiana, U. elliptica, U. elongata, U. gaussenii, U. glabra, U. glaucenscens, U. harbinensis, U. kunmingensis, U. lacianiata, U. laevis, U. lamellosa, U. lanceifolia, U. macrocarpa, U. microcarpa, U. minor, U. parvifolia, U. prunifolia, U. pseudopropinqua, U. pumila, U. szechuanica, U. uyematsui, U. villosa, U. wallichiana*), North America has 6 species (*U. alata, U. americana, U. crassifolia, U. rubra, U. serotina, U. thomasii*) and Mesoamerica two species (*U. ismaelis, U. mexicana*).

Habit
Deciduous or evergreen trees and shrubs reaching heights of 20-40 m. The branchlets are never spinose, but may be corky or winged. Leaves are alternate, with bases typically oblique and margins simply or doubly serrate. Flowers are mostly bisexual, appearing in spring before leaves, though rarely in autumn or winter. Tepals are membranous and usually persistent. The samara is flat, orbicular, obovate, oblong or elliptic, with membranous wings. The seed is positionned at the center or toward the apex of the samara.

Ecology
In Asia, *Ulmus* species are mostly found in broad-leaved forests on slopes and in valleys, with some species occuring in wetlands near streams from 200 to 2900 m a.s.l. In Europe, the three species grow in temperate, broad-leaved forests, either along streams and valleys or in thermophilous coppices, forest edges or hedgerows, from 100 till 1400 m a.s.l. In North America, elm species are likewise found mainly along rivers in alluvial forests and other species-rich deciduous forests, from sea level to 1400 m a.s.l. The two Mesoamerican species occur at elevations from 800-2200 m a.s.l. in high-elevation tropical rain forests or cloud forests, with annual precipitation of 2000-4000 mm.

Distribution
The main center of distribution is East Asia, where China alone harbors 21 species, 14 of which are endemic. The widest distribution is probably that of *U. pumila* from Central Asia to the Korean Peninsula. Most species occur in the mid-elevation mountains of China, Korea and Japan, with one species (*U. lanceifolia*) extending as far south as the Lesser Sunda Islands of Indonesia. *Ulmus* species occur also in Western Eurasia, from the Ural to the Iberian Peninsula, including southern Scandinavia and the British Isles.
The second center of diversity is North and Central America, where species grow in eastern Canada, the United States and northeastern Mexico. Only two species extend further south into Mesoamerica as far as Panama, where their distribution is highly fragmented.





1. The inconspicuous flowers of the European white elm (*Ulmus laevis*) are borne on unusually long peduncles, as here in an alluvial forest on the shores of Lake Morat in Switzeland. (nk)

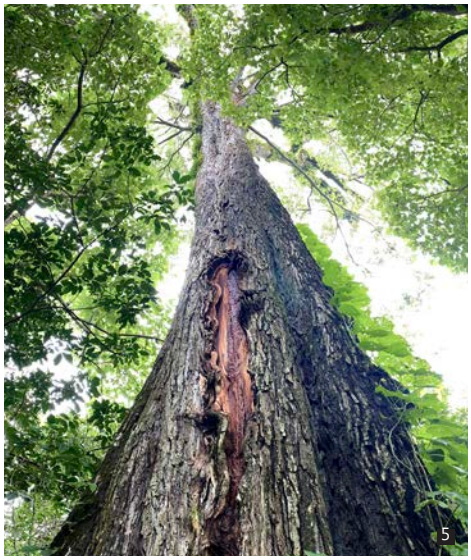
2. The rock elm (*U. thomasii*) of the Midwestern United States and southern Canada has the typical serrate leaf margins found in many elm species of the world, as here near Montreal in Canada. (inat-owenclarkin)



3. As one of the few European tree species, the European white elm (*U. laevis*) develops impressive buttress roots that provide stability in seasonally flooded habitats, as here in Wielkopolska National Park, near Poznan, Poland. (gk)

4. Some species develop corky wings on the branches, as here a field elm (*U. minor*) in Switzerland. (nk)





5. In Central America, the genus is represented by two species. The Mexican elm (*U. mexicana*) grows into a large forest tree and is extremely important for a wide range of species depending on such habitat trees, as here in El Salvador (fsc)

Zelkova Spach

6 species



Age and origin

The oldest known fossils of this genus date back to the early Eocene (55 million years BP). Species of *Zelkova* remained common throughout the temperate Northern Hemisphere until the Pliocene (around 3 million years BP). Due to extensive glaciation in Europe and North America, the genus was eventually restricted to Mediterranean Islands, the Caucasus and far-east Asia.

Extant species

There are six accepted species. Three occur in far-east Asia: *Z. serrata*, *Z. sinica* and *Z. schneideriana*; one is found in south-west Asia (*Z. carpinifolia*) and two are restricted to islands in the Mediterranean Sea: *Z. abelicea* and *Z. sicula*.

Habit

Zelkova species are deciduous trees or shrubs reaching heights of 30-35 m. The branchlets are never spinose, corky or winged. The leaves are alternate, with 2 caducous stipules, leaf margins are serrate to crenate. The plants are monoecious, with flowers appearing at the same time as the leaves. Male and female inflorescence are separate, although female flowers are sometimes intermixed with bisexual flowers. The fruit is a nut-like drupe with a dorsal keel, produced in the leaf axils.

Ecology

In Asia, *Zelkova* species are found in dense, relatively humid mixed broad-leaved forests, in valleys along streams and rivers from 200 to 2500 m a.s.l. In the Mediterranean region, the species grow in small patches within pasturelands in typical maquis vegetation, at elevations of up to 1600 m a.s.l. in Crete and 300–550 m a.s.l. in Sicily.

Distribution

Zelkova has three main centers of distribution: eastern Asia, southwestern Asia and the Mediterranean region. Of the three eastern Asian species, two are endemic to central and eastern China (*Z. sinica, Z. schneideriana*). The third species, *Z. serrata*, has a wider distribution extending from central China through the Korean Peninsula to Japan.

One species, *Z. carpinifolia,* grows in the Colchic and Hyrcanian forests between the Black and Caspian Seas of Türkiye, Georgia, Armenia, Azerbaijan, Iraq and Iran.

The two species with the westernmost distribution are found on the Mediterranean islands: *Z. abelicea* on Crete (Greece) and *Z. sicula* on Sicily (Italy). Both species have a highly restricted distribution, not only because they are island endemics, but also because they are heavily grazed and threatened by habitat alteration.







1. The small, serrate leaves of *Zelkova sicula* in one of the only two known wild populations in southeastern Sicily, Italy. (gk)

2. The tiny, greenish flowers of *Z. carpinifolia* are typical of the genus *Zelkova*. (gk)

3. *Zelkova abelicea* at sunset in the Omalos mountains of western Crete, Greece. (gk)



4. The leaves of *Z. schneideriana* are more slender and have an elongated tip, as observed in Taiwan. (gk)

5. *Zelkova sinica* typically grows in the immediate vicinity of streams and small rivers. The species is now almost entirely absent outside protected areas. Example locality: Gu Tan Gou, China (gk)

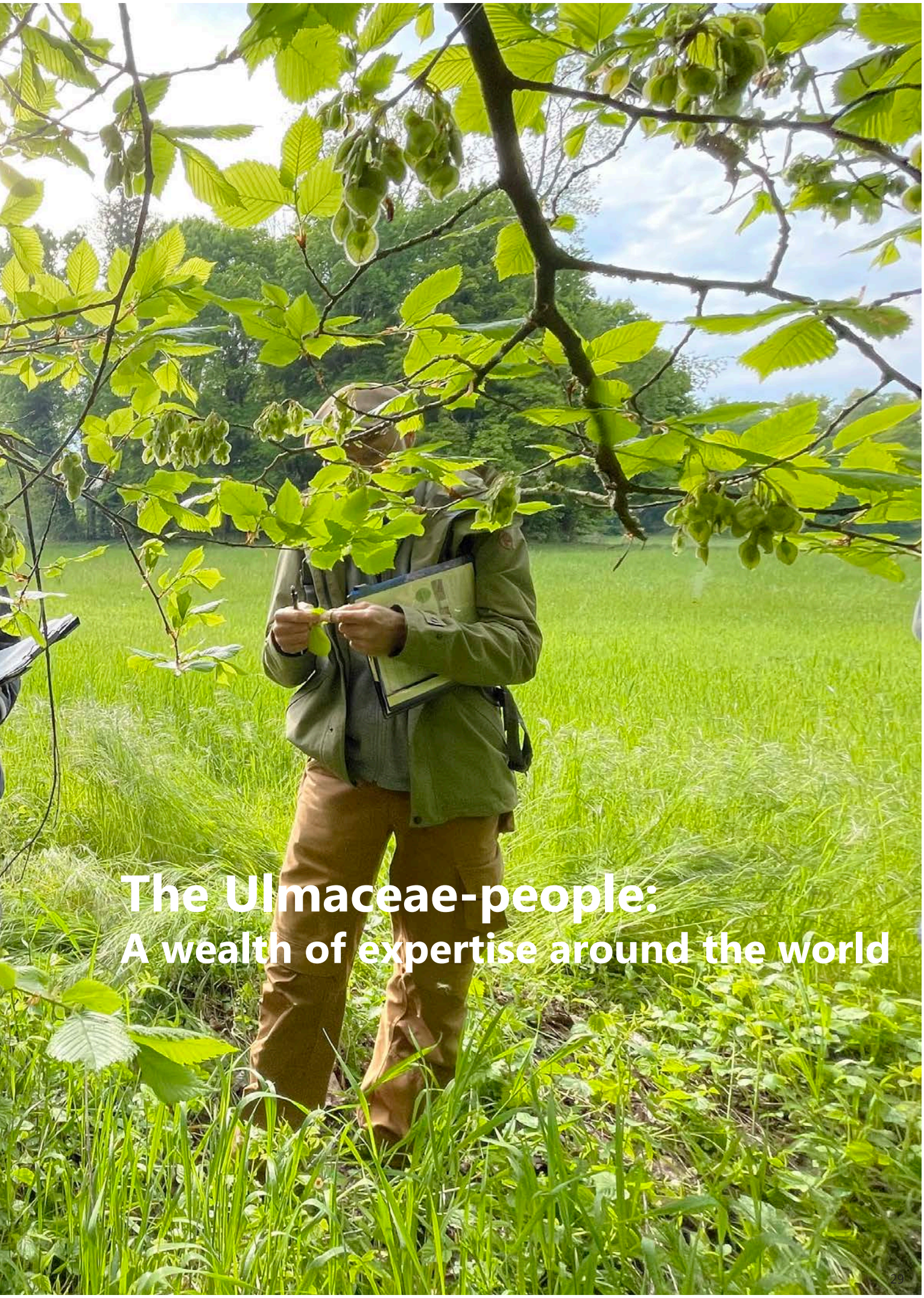


6. A beautiful stand of *Zelkova serrata* in the city of Tokyo, Japan. (gk)





Dr Yann Fragnière, Lena Dermelj and Jacques Sciboz of the Botanic Garden of Fribourg examining a fruiting *Ulmus laevis* at Lake Morat, Switzerland. (gk)



The Ulmaceae-people:
A wealth of expertise around the world

Steven R. Manchester

Florida Museum of Natural History, USA

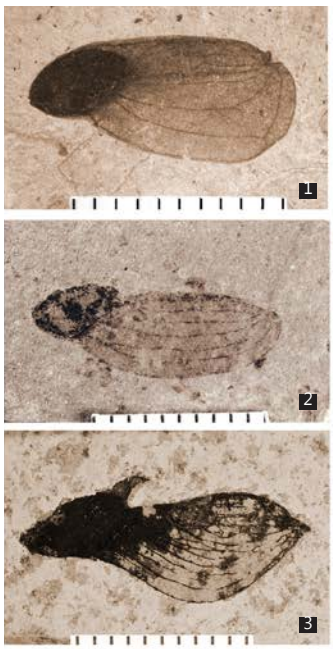
Cedrelospermum

The elm family has an excellent fossil record, including many occurances of the extant genera, *Ulmus* and *Zelkova*. Some of the seven extant genera have not yet been confirmed in the fossil record. In conrast, the extinct genus *Cedrelospermum* was once widespread across the Northern Hemisphere.

I first became interested in the winged fruits of *Cedrelospermum* in the 1970s as a high school student, encountering them in shales while collecting fossil leaves preserved in Eocene shales in Oregon, USA. Prof. William Tidwell, known for his popular book, Common Fossil Plants of Western North America, informed me that he had acquired a special fossil twig specimen bearing attached leaves and the same kind of winged fruits. He mentioned that he had seen similar fruits illustrated in a German paleobotanical textbook by Karl Mägdefrau (1956). This led me to realize that our North American fossils matched those already recognized in Europe a century earlier.

In 1889, Gaston de Saporta coined the name *Cedrelospermum* for these fossil disseminules from the Oligocene of France. Although the Latin name *Cedrelospermum* suggests seeds related to the living genus *Cedrela* (family Meliaceae) the attachment on twigs proved that they were fruits (samaras) rather than seeds, and further research showed that they belong to Ulmaceae rather than Meliaceae. This reassignment to Ulmaceae relied on some detective work to understand the morphology of the fruits and the connected leaves. The leaves are borne in an alternate, distichous arrangement, as in most extant genera of Ulmaceae. Their asymmetry and short, thick petioles also match the family's characteristics. Although they resemble those of *Zelkova*, they are typically narrower. Many North American leaf fossils had previously been identified to *Zelkova*, but their attachment to twigs bearing *Cedrelospermum* samaras rather than the nut-like wingless fruits of *Zelkova*, showed that identification to be incorrect. Additional evidence came from a fossil twig preserved in flowering condition: pollen extracted from its stamens was porate and verrucate, consistent with characteristics expected for Ulmaceae.

In recent years, paleobotanists have extended the known geographic range of *Cedrelospermum* southward to southern Mexico, and eastward from France to Romania, with newly recognized occurrences in Asia (southwestern China and Tibet).

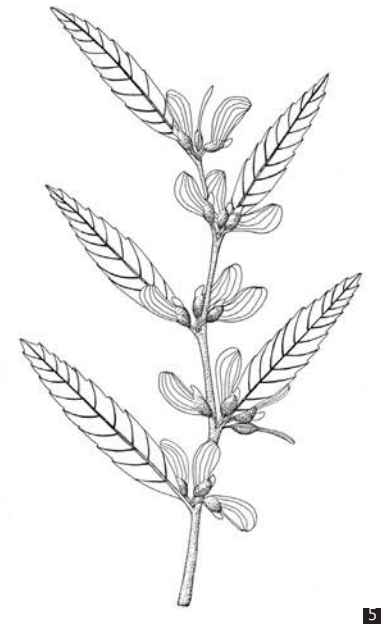


1. Fruit of *Cedrelospermum leptospermum* Manch. from the Upper Oligocene of Rott, near Bonn, Germany, showing the oval nutlet and wing with six veins converging toward the distal stigmatic cleft. A line of suture of the two carpels runs between the nutlet and stigmatic cleft. Natural History Museum, London, V 56922A.



2. Fruit of *Cedrelospermum lineatum* (Lesq.) Manch. from the late Eocene Florissant flora, Colorado, USA. University of California Museum of Paleontology.

3. Fruit of *Cedrelospermum asiaticum* Jia et al. from the Oligocene deposits of Maguan, Yunnan, China.



4 and 5. Photo and diagram of a twig of *Cedrelospermum lineatum* from the middle Eocene Green River Formation of Utah, USA.

Boris Villanueva Tamayo

Herbarium, José Celestino Mutis Botanical Garden, Bogotá, Colombia

Ampelocera percyhernandezii

The new tree species *Ampelocera percyhernandezii* was discovered during explorations in dry forest remnants located far from populated areas in the central Colombian Andes. Only about 5 % of this ecosystem remains in Colombia, and the forest where the studied populations occur is among the best preserved. In this area, permanent research plots were established to monitor populations of this and other threatened species from this ecosystem.

A key collaborator in these investigations was Percy Hernández, a skilled local parataxonomist and long-time resident of the region, whose knowledge has been fundamental for the protection of these forests against illegal logging and charcoal production. The new species produces its flowers over very short periods; in the absence of rainfall, only staminate flowers are produced, whereas under favorable conditions, small ovaries emerge after the anthers wither.

I remember two anecdotes. The first took place during a course we conducted in this low-hill forest. By accident, I slipped and injured my ankle. Don Percy applied a plant-based preparation that allowed me to keep walking for the rest of the day. When I finally reached a health facility, I learned that my foot was actually fractured.

The second anecdote occurred later, when the article was already well advanced. I visited the astronomical observatory built during the colonial period by José Celestino Mutis and his collaborators in 1803. I opened the last printed volume of the plates from the Real Expedición Botánica al Nuevo Reino de Granada, and the very first page I turned revealed the illustration of this new species – allowing it to be directly referenced.



1. Don Percy Hernández, discoverer of the new *Ampelocera* species in central Colombia, pointing at one of the trees in its natural habitat. (bvt)

2. and 3. The small, inconspicuous flowers of *A. percyhernandezii* are typical for the genus *Ampelocera*. (bvt)

4. The species was descovered in 2024 in species-rich remnants of seasonally dry forests in the upper Magdalena river valley in central Colombia, at elevations of 250–600 m a.s.l. (bvt)







Maximilian Gödecke

Photographer, Berlin, Germany

Zelkova abelicea

We were driving near Gerakari in the late afternoon, between rocky slopes and the first foothills of the mountain range, when the fog grew thicker and thicker. Jonas cautiously steered our small Fiat up the narrow, gravelly track, and the higher we drove, the quieter everything became. Once we reached the top, we quickly realized we had landed in the wrong climate. Since we hadn't brought rain gear, we cut three holes into large black garbage bags and pulled them over ourselves. The wind alternately drove coarse and fine drops horizontally through the shifting white mist, and for a moment, it felt like if we had stepped into another landscape – one that reveals itself only when you are not actively looking for it.

The fog lay over everything like a veil. Rocks, shrubs and trees emerged from the white only at the last moment, and among them stood the zelkovas, as if they were ancient figures patiently waiting for someone to listen to their stories. These trees have a character of their own: gnarled, tough, resilient – and yet full of dignity. In this mixture of moisture, wind and silence, they seemed like beings who have lived up here much longer than any thought of research.

Every now and then, we heard the faint ringing of sheep bells, somewhere far beyond the fog – a sound that reminded us there was still a world on the other side of the white wall.

We stood there, wet, freezing and fascinated. The zelkovas were not just botanical curiosities – on that day, they were our hosts.

This place has stayed with me – not because of its beauty in a classical sense, but because of the atmosphere that permeated everything: a feeling of having briefly been part of a hidden world.





Laurence Fazan

Botanic Garden of the University of Fribourg, Switzerland

Zelkova abelicea

For over a decade, I studied and worked on improving the knowledge on and conservation of *Zelkova abelicea*, a rare and endangered tree species growing only in specific and often remote areas in the mountains of Crete. My work took me to secluded slopes – places known only to shepherds, goats and sheep – where I investigated this fascinating species and the conditions in which it grows. Along the way, I picked up some Greek and developped a deep appreciation for the region.

As part of my PhD, I explored how *Z. abelicea* responds when browsing pressure is removed, and investigated its reproductive strategy, including seed sterility. But the real plot twist came when I stumbled upon something unexpected: tiny white larvae were deforming the male flowers of the trees!

Curiosity turned into a full-blown and fascinating adventure. Finding the larvae was not enough – we needed the adult insects to identify the species. After several failed attempts to directly capture the adult insect using nets and insect traps, we resorted to collect flowers with larvae inside and had them sent by express mail to Switzerland. I then placed the larvae in mesh-covered pots on my balcony, where they exited the flowers and buried themselves in the soil where they pupate throughout summer, autumn and winter before emerging as adults. I waited (im)patiently for nearly a year, checking the pots regularly for signs of emergence. Finally, 7(!) adults appeared. Then came the challenge of finding a specialist – one of the few in the world – who could identify them.

The result? A new species of gall midge (Cecidomyiidae): *Contarinia ampelitsiae*, named after the Cretan word for *Z. abelicea*: Αμπελιτσιά. The discovery of this new species shows a glimpse into the incredible and still to discover biodiversity and ecological processes associated with these old trees. In this case we are talking about an endemic insect growing on an endemic plant.


1

1. Laurence Fazan taking measurements in a very old stand of *Zelkova abelicea* during her fieldwork in Crete. (sp)

2. The botanist as an entomologist. Investigating insect diversity around *Zelkova abelicea* trees. (jl)

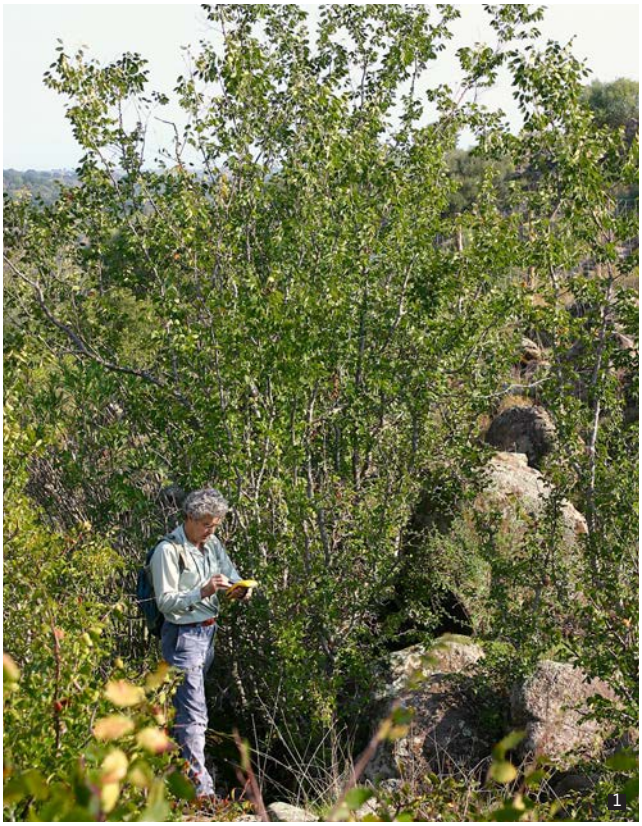
3. A male gall midge of *Contarinia ampelitsiae*. The larvae develop in the male flowers of the Cretan zelkova. This behavior is unique as gall midges usually develop within female flower structures. (lf, photo taken from Fazan et al. 2023)


2


3

Giuseppe Garfì

Institute of Biosciences and BioResources, National Research Council, Italy





1. Giuseppe Garfì measuring the exact position of this rather tall Sicilian zelkova in southeastern Sicily. (sp)

2. The populations grow along seasonnaly water-bearing courses, alongside other rare plant species, such as *Isoetes durieui*. (gg)

3. The serrate margin of the leaf of *Z. sicula* is characteristic for the entire genus *Zelkova*. (gk)

***Zelkova sicula*, an incredible finding**

Within the European forest flora *Zelkova sicula* is probably the last tree species to have been described as new to science. Its discovery dates back to 1991, when during a vegetation survey some unusual shrubs and treelets were observed within a degraded cork oak forest. At the time, it was assumed to be merely an uncommon plant unfamiliar to me, as I was the young forest researcher engaged in the task. Instead, it marked the beginning of an intriguing scientific story. Far from expecting that, – at the end of the 20th century a previously undescribed tree could still be found in Europe –, all attempts at identification using regional floras proved unsuccessful. This difficulty was compounded by the lack of floral material – one of the key elements in plant taxonomy – since heavy grazing prevented the development of reproductive structures. Some specimens were therefore sent to Prof. Pierre Quézel (University of Aix-Marseille), a leading authority in Mediterranean botany. He immediately recognised diagnostic features typical of the genus *Zelkova*, but these did not match any of the five known species worldwide. Hoping that a flowering would allow a more definitive identification, the researchers waited another year, without success. Eventually, relying on Quézel's expertise, they decided not to delay further and proceeded to publish the finding in a specialist journal, treating it somewhat like a "poker game" based on accumulated evidence. Thus, a new species, named *Zelkova sicula* (i.e. from Sicily) was added to the list of the European tree flora. Six years later, the flowering of a few plants confirmed we had won our bet.

Until 2009, the known small population stayed unique worldwide, when a second population was discovered a few kilometres away. This fortunate event has not been repeated since, so today the Sicilian zelkova still consists of just two tiny populations, making it one of the rarest tree species on the planet.



Yi-Gang Song

Shanghai Chenshan Botanical Garden, China

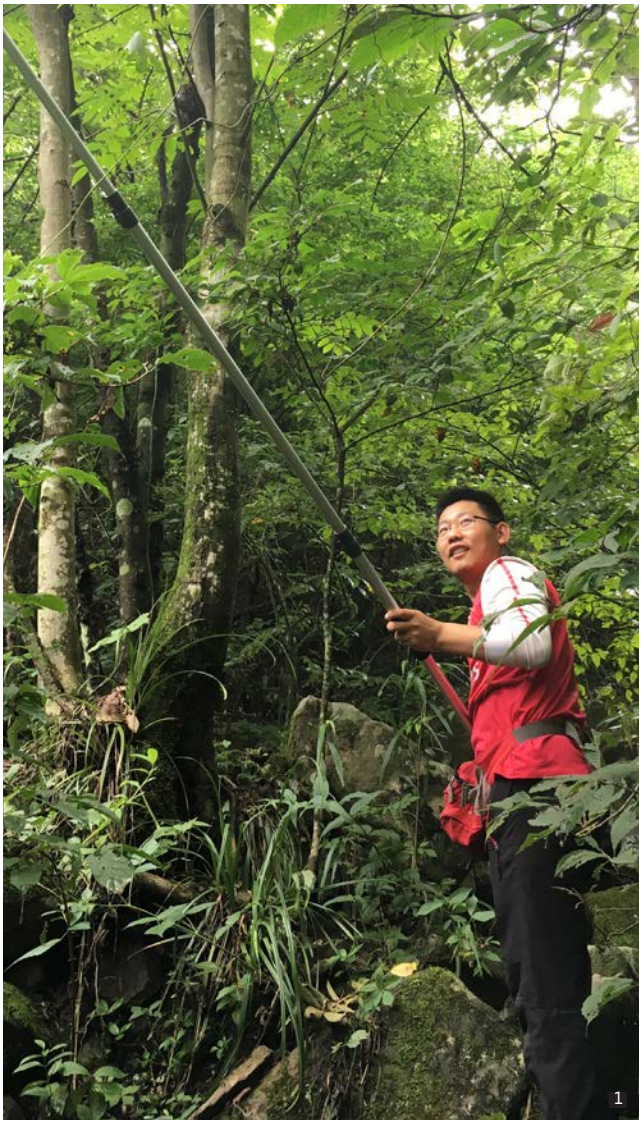
***Zelkova sinica*, the only species in this genus with spherical fruits**

Wood of *Zelkova* shows a beautiful texture, excellent physical properties and good processing performances. In addition, *Zelkova* is a auspicious symbol in Chinese culture. Thus, the genus has significant economic and cultural value in China.

Zelkova sinica is an endemic tree species in China and typically growing near rivers at elevations between 300 and 2500 m a.s.l. It is mainly distributed in subtropical deciduous forests around the Qinling-Daba Mountains of China, with only a few populations extending into the southern Taihang Mountains.

We assessed this species as Vulnerable, due to its limited distribution and the small number of populations. *Zelkova sinica* has also been of high commercial importance because of its high-quality, reddish wood. Large individuals were systematically cut in the past for use in the construction and furniture industries.

It is closely related to *Zelkova schneideriana*, and is distinguished by features such as its spherical fruits. Ancient trees of *Zelkova sinica* can still be found in protected forests and in relatively inaccessible mountain areas.


1

1. Yi-Gang Song collecting branches of *Zelkova* in China. (jy)

2. A beautiful Chinese zelkova tree in the Funiu Mountains, Henan, China. (ys)

3. The typical spherical fruits of *Zelkova sinica*. (ys)


2


3

Sébastien Bétrisey

Natural History Museum Fribourg, Switzerland

Zelkova serrata

When I started working at the Botanic Garden of the University of Fribourg in 2011, I had no idea of the adventures I would later experience in faraway countries in search of extraordinary trees. After participating in an initial study on the genetic diversity of the genus *Zelkova* in ex situ collections kept in botanical gardens, I was finally able to carry out my first field mission. The ultimate opportunity for a young botanist who loves video games and manga, the destination was Japan.

I was greatly surprised to discover the streets of Tokyo flashing frantically with neon lights and, above all, lined with alleys of *Zelkova serrata*. It was precisely this majestic tree that I had come to study. But it wasn't these specimens, planted for their beauty or the shade they provide, that I was searching for. To avoid cultivars of uncertain genetic origin, I had to leave the city and head into remote natural environments to locate *Zelkova* trees in their natural habitat within ancient, undisturbed forests.

A successful field expedition depends on several factors: equipment, careful planning, a good dose of luck, but above all, reliable contacts on site. I still remember the kindness and extraordinary knowledge of their flora displayed by the researchers and university professors who accompanied me and helped me in my fieldwork. I got to know colleagues, but often left behind friends.

I remember all the people I met, but also many trees, such as a hundred-year-old *Zelkova*, guardian of a temple and silent witness to another time, when certain majestic trees were considered sacred and served as a refuge for spirits. The discovery of natural *Zelkova* forests left me with lasting memories. In the following years, I was able to explore South Korea and China in order to collect genetic material and asses the conservation status of the Asian species of *Zelkova*. I was fortunate enough to work on the conservation of relict trees for eight years, and during that time I was part of a large family of researchers who were geographically very distant, but whose bonds were as strong as the gnarled roots of a *Zelkova*.







1. This *Zelkova serrata* grows close to Tataoki River in Japan. (sb)

2. The shinto shrine in Hita City on the island of Kyushu, Japan, with an old *Zelkova serrata*. (sb)

3. Sébastien Bétrisey during his fieldwork in South Korea in front of a venerable *Zelkova serrata*.

Yann Fragnière

Botanic Garden of the University of Fribourg, Switzerland

***Ulmus laevis*, a relict of riparian floodplain forests**

In a country as thoroughly studied as Switzerland, how could a tree remain mysterious for so long? This question arose when we unexpectedly encountered some specimens along the banks of the Sarine River in the canton of Fribourg: the European white elm (*Ulmus laevis*). We wanted to uncover the origin of this species. This tree is a typical inhabitant of riparian forests across parts of Europe. Yet in Switzerland, positioned at the very margin of the species' natural distribution range, *U. laevis* is very rare. Its presence in the country was long regarded with skepticism. Some considered it an introduced or cultivated species, rather than a naturally occurring one.

Our research aimed to clarify this ambiguity and provided evidence that *U. laevis* does indeed grow naturally in Switzerland. However, its situation is precarious. In the 19th century, major hydrological interventions, such as the channelization of large rivers and the stabilization of lake water levels, profoundly altered the alluvial dynamics of the Swiss lowlands. These changes disrupted the ecological conditions required for the natural regeneration of *U. laevis.* As a result, the species now survives primarily as a relict, confined to remnants of ancient floodplain forests whose natural processes have been significantly modified. Under such altered conditions, regeneration is sporadic and often insufficient to ensure the long-term viability of populations.

Today, thanks to our project, *U. laevis* is recognized as native. It is one of the rarest and most threatened tree species in Switzerland. Our findings have contributed to a paradigm shift: *U. laevis* is no longer seen as a species of secondary importance, but as a key element in the conservation of riparian forest ecosystems.



1. Mostly growing close to water bodies, as here at Lake Morat in Switzerland, *Ulmus laevis* forms impressive buttress roots. (yf)

2. Two of the main characters are the stalked fruits and the fringed margins of the fruits. (yf)

3. In autumn, the leaves of *U. laevis* turn into a vibrant golden colour. (yf)





Frank Sullyvan Cardoza Ruiz

Tropical Agricultural Research and Higher Education Center, El Salvador



1. A majestic Mescal stands in a species-rich Salvadoran forest. (fsc)

2. Frank Sullyvan standing in front of another species from the Ulmaceae family growing in Central America: *Phyllostylon rhamnoides*. (fsc)

Mescal (*Ulmus mexicana*), an ancient giant

El Salvador is the smallest of the 22 countries in continental America, with an area of 21'041 km^2. However, its flora and fauna are remarkable, and its forests are home to fascinating tree species. In terms of its tree flora, the country has 1216 tree taxa, of which 1003 are native, including both subspecies and varieties.

There is one particularly fascinating tree species that is of special interest and can be considered emblematic and imposing, and which all Salvadorans should know: the tree called "Mescal," "Naranjillo" or "Duraznillo" (*Ulmus mexicana*). It grows at altitudes of 800–2000 m a.s.l. in cloud forests and is found from Mexico to Panama. It is the tallest and one of the longest-lived tree species in El Salvador, potentially reaching up to 75 meters in height and living for aroound 500 years. It is also among the 54 tree species in danger of extinction in the country. Due to its large size and dense canopy, *U. mexicana* plays a crucial ecological role, providing benefits such as water regulation for freshwater supply, carbon sequestration and support wildlife biodiversity.

In El Salvador, only few individuals remain, restricted to sites such as El Imposible National Park, Montecristo National Park, Ilamatepec Volcano, Quezaltepec Volcano and parts of the department of Usulután. I vividly remember my first encounter. Instantly, the tree's imposing height and shade stopped me in my tracks. Captivated, I contemplated its immensity, approaching the trunk to look up into the canopy. At that moment, time seemed to stand still and after a few minutes, with immense satisfaction, I captured photographs that reveal the fascinating biodiversity of El Salvador's landscapes. The "Mescal" is a silent giant, an immemorial witness and an ancestral guardian of the forest. Its crown is a green altar that seems to touch the sky, hosting tiny worlds that form vibrant sanctuaries of life. Conservation efforts are essential to ensure the survival of this key species. Let us embrace its immensity as a covenant entrusted to us. The forests call us, and in their sacred and wise echo, we can reconnect with the essence of our existence.



Rui-Sen Lu

Jiangsu Province and Chinese Academy of Sciences, Nanjing, China

***Ulmus chenmoui*, an endangered species from eastern China**

Eastern China is one of the most economically developed areas in the country. It supports nearly 30 % of the China's population with less than 10 % of its land area. This area is also home to over 7000 vascular plant species, representing more than 15 % of China's total vascular diversity.

Only three populations of the endangered elm *Ulmus chenmoui* exist in the Langya Mountains (Anhui Province) and the Baohua Mountains (Jiangsu Province) in eastern China. During field surveys, fewer than 50 individual trees of *U. chenmoui* were recorded. The species typically co-occurs with trees such as *Acer henryi, Phoebe sheareri, Celtis sinensis, Zelkova schneideriana, Pistacia chinensis* and *Liquidambar formosana*, forming a deciduous broad-leaved forest.

To conserve this endangered species, Nanjing Botanical Garden Mem. Sun Yat-Sen has collected seeds from these populations, germinated them and successfully cultivated the seedlings. A stakeholder meeting on the conservation of *U. chenmoui* was held in 2024 at Baohua Mountain National Forest Park under the guidance of Botanic Gardens Conservation International (BGCI) and the Jiangsu Forestry Science and Technology Innovation and Promotion Project. More than 400 individuals have been ex situ conserved in the botanical garden. In the future, the conservation team plans to reinforce the three populations.



1. Rui-Sen Lu in a lush forest with *Ulmus chenmoui, Acer henryi* and *Liquidambar formosana*. (ml)



2. As in many elm species, the leaf base is asymmetrical. (rl)



3. The winged samaras of this species are approximately 25 x 17 mm and ripen normally in April. (rl)

Gregor Kozlowski

Botanic Garden of the University of Fribourg, Switzerland

***Zelkova*, elms, relict trees … and us**

The adventure with the Ulmaceae began more than fifteen years ago. It started with the endemic Mediterranean zelkova species – *Zelkova abelicea* and *Zelkova sicula*. Together with researchers and students from Sicily, Crete, and the University of Fribourg, our initial goal was a traditional one: to study the distribution, genetic diversity, and ecology of these rare and, at the time, little-known trees.

However, something unexpected happened very quickly: these trees captivated us. Each discovery opened new doors, revealing further questions and hidden secrets. From these early projects, new ideas and collaborations emerged, soon extending to elms and other relict trees from related plant families. Over the years, this developed into a network of more than thirty people: scientists, conservationists, foresters and friends from over fifteen countries, spanning Europe, the South Caucasus, East Asia and the Americas.

It was often the small discoveries that brought us the greatest joy. Among the highlights was the discovery of a new insect species, *Contarinia ampelitsiae*, which forms galls on the flowers of *Zelkova abelicea*. Equally significant was the confirmation that *Ulmus laevis* is indeed native to the forests of Switzerland and is therefore worthy of protection.

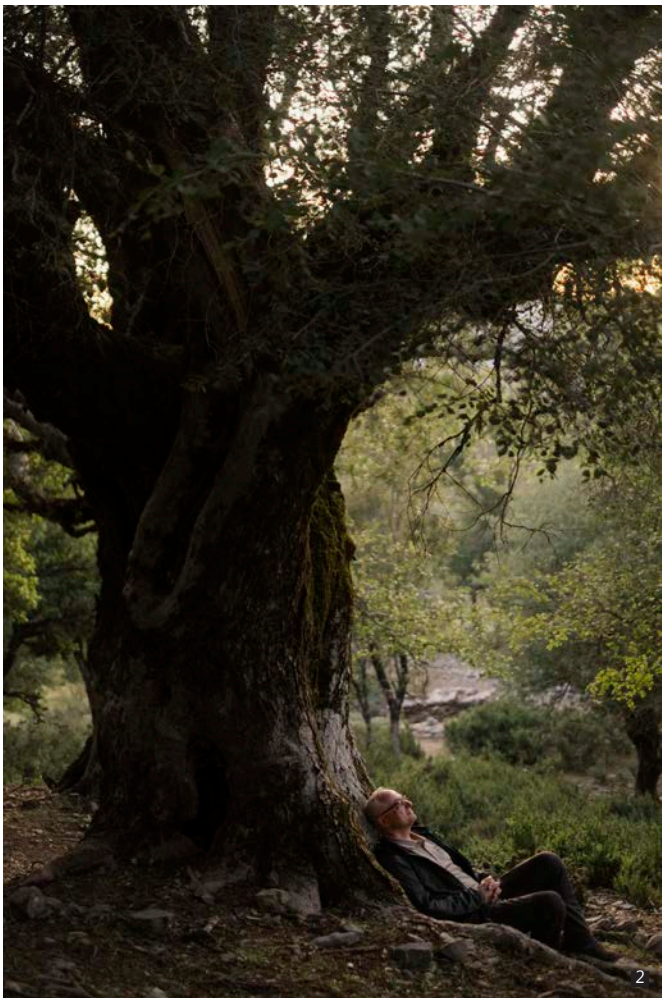
Time and again, there is that special feeling – when observing something never before described by human eyes. For a brief moment, one feels like an explorer, even if it is only a tiny detail in the life of these great, ancient tree organisms.

What have we learned over all these years? For me personally – and even if it sounds almost sentimental – my sense of wonder at the complexity of life has deepened. Plant families composed entirely of trees, whose members have been scattered across continents by major climatic and tectonic events, offer a unique perspective. They vividly reveal the astonishing diversity of survival strategies and the resilience of life itself.

With this book, we wished to make that diversity visible – not only the diversity of the trees themselves, but also the diversity of the people who study them, who learn to see them with ever-fresh eyes. And above all, one thing remains: curiosity. I look forward with great anticipation to what we will learn in the decades to come about these remarkable trees.



1



2

1. An impressive individual of Cretan zelkova, probably hundreds of years old. (gk)

2. Gregor Kozlowski reflects on the past 15 years of research on Ulmaceae – here in Crete, in a large *Zelkova abelicea* grove. (mg)

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Opposite page: *Zelkova abelicea* at sunset in the Omalos mountains of western Crete, Greece. (gk)



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