

important for species identification in some genera (e.g., *Terminalia*), whilst in others, flowers are important (e.g., *Combretum*).

The majority of Combretaceae produce poor-quality timber, although *T. ivorensis* and *T. superba* are internationally important timbers and have been grown in West African plantations; others (e.g., *Lumnitzera* in Malaysia and *T. arjuna* in India) have important local timber uses. The family produces important ornamentals (e.g., *Quisqualis indica*, *Combretum grandiflorum*) and widely planted pantropical street trees (e.g., *T. catappa*). The fruits of some *Terminalia* species (known as myrobalans) are important in tanning, whilst other combretaceous species are important as local foods, dyes, and medicines.

See also: **Tropical Forests:** Monsoon Forests (Southern and Southeast Asia); Tropical Dry Forests; Tropical Moist Forests.

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## Lauraceae

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## Introduction

The Lauraceae is a family (about 50 genera and about 3000 species) (Table 1) of mainly subtropical

and tropical trees (except the genus *Cassytha* which is an herbaceous parasite), and is most diverse in the American and Asian tropics, although many species occur in Australia and Madagascar. Some genera range into the temperate region, e.g., *Sassafras* in North America, *Lindera* in Japan, and *Beilschmiedia* in New Zealand. The family is primarily found in lowland and montane rainforest, and can occupy a wide range of elevations from sea level to páramos in South America. In some habitats the Lauraceae is one of the most common trees families, for example, in the foothills and at mid-elevations in the Andes and as dominants in the relict laurel forests of the Canary Islands and Madeira.

## Classification

Morphological and molecular data indicate that the Lauraceae is a monophyletic family, although classification with the family is less clear. Despite its ecological importance in tropical ecosystems, the Lauraceae is poorly known, since material is difficult to collect, the flowers are inconspicuous, and fruits and flowers are needed for accurate identification of most species. This creates problems for the delimitation of both genera and species, and thus absolute statements about generic distribution are difficult to make, particularly for genera that have widely disjunct distributions (e.g., *Apollonias* between India and the Canary Islands).

Traditional Lauraceae classifications have placed the parasitic genus *Cassytha* in its own subfamily (Cassythoideae), and treated the remaining genera as a second subfamily (Lauroideae). Within the Lauroideae, morphological characters (e.g., flower and wood anatomy) have been used to define three tribes: (1) Laureae (e.g., *Laurus*); (2) Perseeae (e.g., *Persea*); and (3) Cryptocaryeae (e.g., *Beilschmiedia*). However, molecular analysis of the family suggests that *Cassytha* should be placed with either *Hypodaphnis* or *Neocinnamomum*, and that the Lauroideae tribes, as currently defined, are not monophyletic.

## Reproduction

Lauraceae flowers are insect-pollinated, usually with modified stamens that secrete either odor or nectar, and individual trees are hermaphrodite, monoecious, or dioecious. In addition to dioecy, there are mechanisms to promote outcrossing, including the occurrence of two flower types with different daily patterns of stigma receptivity and pollen presentation, as found in *Persea americana*. The Lauraceae

**Table 1** Distribution of genera in the family Lauraceae

<i>Genus</i>	<i>Approximate number of species</i>	<i>Distribution</i>
<i>Actinodaphne</i>	100	Asia
<i>Aiouea</i>	20	Central and South America
<i>Alseodaphne</i>	50	Tropical Asia
<i>Anaueria</i>	1	Amazonia
<i>Aniba</i>	40	Tropical America
<i>Apollonias</i>	2	Canary Islands; India
<i>Aspidostemon</i>	15	Madagascar
<i>Beilschmiedia</i>	250	Pantropical
<i>Brassiodendron</i>	2	Pacific islands; Australia
<i>Caryodaphnopsis</i>	15	Asia; Central and South America
<i>Cassytha</i>	20	Pantropical
<i>Chlorocardium</i>	2	South America
<i>Cinnadenia</i>	2	Southeast Asia
<i>Cinnamomum</i>	350	Tropical and subtropical Asia; Australia; Pacific islands
<i>Cryptocarya</i>	350	Pantropical
<i>Dahlgrenodendron</i>	1	South Africa
<i>Dehaasia</i>	35	Asia
<i>Dicypellium</i>	2	East Amazonia
<i>Dodecadenia</i>	1	Southern Himalaya
<i>Endiandra</i>	100	Asia; Australia; Pacific islands
<i>Endlicheria</i>	40	Tropical America
<i>Eusideroxylon</i>	1	Malesia
<i>Gamanthera</i>	1	Costa Rica
<i>Hexapora</i>	1	Malaysia
<i>Hypodaphnis</i>	1	West Africa
<i>Iteadaphne</i>	2	Southeast Asia
<i>Laurus</i>	2	Mediterranean Europe; Canary Islands; Azores
<i>Licaria</i>	40	Tropical America
<i>Lindera</i>	100	Asia; Australia; North America
<i>Litsea</i>	400	Asia; Australia; Pacific islands
<i>Mezilaurus</i>	20	Tropical South America
<i>Nectandra</i>	120	Tropical and subtropical America
<i>Neocinnamomum</i>	6	South China; North Vietnam
<i>Neolitsea</i>	100	Asia
<i>Nothaphoebe</i>	40	Asia, mainly Malaysia and Indonesia
<i>Ocotea</i>	350	Tropical and subtropical America; Madagascar; Africa; Canary Islands
<i>Paraia</i>	1	Amazonia
<i>Parasassafras</i>	2	Bhutan; Myanmar; China
<i>Persea</i>	200	Tropical to temperate America and Asia; Canary Islands
<i>Phoebe</i>	100	Asia
<i>Phyllostemonodaphne</i>	1	Southeast Brazil
<i>Pleurothyrium</i>	45	Central and South America
<i>Potameia</i>	30	Madagascar; Asia
<i>Potoxylon</i>	1	Borneo
<i>Povedadaphne</i>	1	Costa Rica
<i>Ravensara</i>	30	Madagascar
<i>Rhodostemonodaphne</i>	20	Tropical South America
<i>Sassafras</i>	3	North America; China
<i>Systemonodaphne</i>	1	Guianas; Amazonia
<i>Umbellularia</i>	1	North America
<i>Urbanodendron</i>	3	Southeast Brazil
<i>Williamodendron</i>	3	Central and South America

usually have a unilocular ovary that produces a single-seeded drupe. The fruit may be free of the fruit stalk or partially or entirely enclosed by the receptacle.

Lauraceae fruits are primarily dispersed by specialist frugivorous birds, particularly bell birds, fruit

pigeons, quetzals, and toucans, with approximately 80% of the diet of some species comprising lauraceous fruits. In the majority of cases the whole fruit is swallowed and the seed then regurgitated a short distance from the parent tree. Nonspecialist birds are important dispersers in temperate regions, whilst

mammals (e.g., squirrels and monkeys) and fish may also be important dispersers.

## Economic Uses

Historically, the Lauraceae is a very important economic family, especially the genus *Cinnamomum*, as a source of spices, e.g., cinnamon (*C. verum*), cassia bark (*C. cassia*) and laurel (*Laurus nobilis*), perfume oils, e.g., rosewood oil (*Aniba roseodora*) and sassafras oil (*Ocotea odorifera*), and pharmaceuticals, e.g., camphor (*C. camphora*). However, the most internationally important product produced today is the avocado fruit (*Persea americana*). Lauraceae wood is widely used locally, although a few are internationally important as high-quality timbers for furniture making or for resistance to salt water, e.g., greenheart (*Chlorocardium rodiaei*), Borneo ironwood (*Eusideroxylon zwageri*), and Queensland walnut (*Endiandra palmerstonii*). Some species (e.g., *Ocotea bullata*), once internationally important, are now protected because of past over-exploitation.

See also: **Ecology:** Plant-Animal Interactions in Forest Ecosystems. **Medicinal, Food and Aromatic Plants:** Medicinal and Aromatic Plants: Ethnobotany and Conservation Status. **Tree Physiology:** Physiology of Sexual Reproduction in Trees. **Tropical Forests:** Tropical Moist Forests; Tropical Montane Forests.

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## Lecythidaceae

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## Introduction

The Lecythidaceae is a pantropical family of trees found in the tropics of Central and South America, southeast Asia, and Africa, including Madagascar (Table 1). The family is divided into five subfamilies: (1) the Planchonioideae, with six genera, the best known of which is *Barringtonia*, and 59 species in tropical Asia, Malaysia, northern Australia, the Pacific Islands, and Madagascar; (2) the Foetidoidae, with a single genus, *Foetidia*, and 17 species in Madagascar, Mauritius, and East Africa; (3) the Napoleoneoideae, with two genera, *Crateranthus* and *Naopoleonea*, and 11 species in West Africa; (4) the Scytopetaloidae, with a single species, *Asteranthos brasiliensis*, in the Negro and Orinoco river basins of Brazil and Venezuela and six genera and as many as 21 species in Africa; and (5) the Lecythidoideae of the western hemisphere. This article focuses on the New World species of Lecythidaceae.

New World Lecythidaceae range from Veracruz, Mexico (*Eschweilera mexicana*) to Paraguay (*Cariniana estrellensis*). The Caribbean harbors only *Grias cauliflora*, a species found in Jamaica, Central America, and northwestern South America. Several species of *Eschweilera* occur on Trinidad and Tobago, but these islands are South American, both geologically and in their floristic affinities.

Neotropical Lecythidaceae are best known for the Brazil nut of commerce (*Bertholletia excelsa*); for the cannon-ball tree (*Couroupita guianensis*), which is planted as a botanical curiosity in tropical and subtropical botanical gardens; and because species of the family are often ecological dominants in Amazonian forests.

## Taxonomy and Genetics

In tropical America, there are 10 genera and 202 known species of Lecythidoideae and a single species, *Asteranthos brasiliensis*, of the African centered Syctopetaloidae. The largest genus is *Eschweilera* with 85 species followed by *Gustavia* (41), *Lecythis* (26), *Couratari* (19), *Cariniana* (15), *Grias* (7), *Corythophora* (4), and *Couroupita* (3). *Allantoma lineata*, *Asteranthos brasiliensis*, and *Bertholletia excelsa* belong to monotypic genera.

Molecular studies have demonstrated that the Lecythidaceae are monophyletic if members of the