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Laurales

Angiosperms

Plant classification

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The Laurales are an order of flowering plants comprised of seven families that contain 2500-2800 species in 85-90 genera. Most Laurales are tropical trees. The order is part of the earliest radiation of flowering plants and is the sister group of the Magnoliales. Lauralean fossils date back to the Early Cretaceous. This article presents each family, followed by the few morphological characters that unite subgroups of families within the order. The absence of a character that would unite all Laurales historically has led to much controversy about the order's circumscription, with several basal angiosperm families, such as Amborellaceae (this is now considered the sister to all other angiosperms), Trimeniaceae, and Chloranthaceae, variously being included or excluded in Laurales. The monophyly of the seven families now considered to form the Laurales first became apparent based on molecular data.

Lauraceae

By far the largest lauralean family are the Lauraceae, with 2200-2500 species in 55 genera (Rohwer, 1993). Lauraceae generally are large trees with highly typical flowers that have tepals and stamens arranged in three-parted whorls and stamens with valvate anthers. In terms of species richness and morphological diversity, the family is centered in tropical America and Australasia; it is poorly represented in continental Africa, but flourishes in Madagascar. Relatively few species, such as spice bush, *Lindera benzoin*, sassafras, *Sassafras albidum*, and true or bay laurel, *Laurus nobilis*, now survive in temperate zones, but during Paleocene and Eocene warmer climates Lauraceae were abundant in the northern landmass of Laurasia. The fossil record of the family goes back 120 Ma, and at least 500 species of Lauraceae are known from the Early Cretaceous through to the Late Tertiary (Eklund and Kvacek, 1998, Eklund, 2000).

A genus whose membership in the family was unclear before the advent of molecular data is the herbaceous parasite *Cassytha*. *Cassytha* comprises 16-20 species in Africa, Southeast Asia, and tropical Australia that have leafless twining stems linked to the host by small haustoria. Molecular data show that *Cassytha* belongs in Lauraceae where its exact phylogenetic position, however, is still unknown (Chanderbali et al., 2001).

The family's great economic importance has three sources. One is the high content of ethereal oils in the wood and leaves of many Lauraceae, which are sources of perfumes, spices, and flavourings, such as camphor and cinnamon. Another is their hard wood, which makes them one of the most valuable sources of tropical timber. Third is the avocado, the oil-rich fruit of *Persea americana*, domesticated several thousand years ago in Central America and now cultivated in tropical and subtropical climates world wide.

Monimiaceae

Monimiaceae comprise about 220 species in 18-25 genera. They are shrubs or treelets occurring in the tropics and subtropics of the Southern Hemisphere. Until recently, the family appeared morphologically unusually heterogenous due to the inclusion of extraneous elements, such as Amborellaceae, Atherospermataceae, Siparunaceae, and Trimeniaceae. Molecular data have shown that a monophyletic Monimiaceae consist of 18-25 genera closely related to the small genus *Monimia* from Mauritius and Réunion (Renner, 1998). By far the largest genus is *Tambourissa* with some 50 species in Madagascar, the Mascarenes, and the Comores (Lorence, 1985). The family's fossil record goes back to the Late Cretaceous of Antarctica. The wood of a few species is used for timber and the leaves for medicinal teas.

Hernandiaceae

Hernandiaceae consist of about 46 species in four genera of shrubs, treelets, and lianas (Kubitzki, 1993a). The largest genus, *Hernandia* (including *Hazomalania*) occurs throughout the tropics, and several of its species are extremely widespread due to transoceanic dispersal of their floating fruits. *Illigera* has 13 species in China, Indochina, and Malesia, two in Africa, and one in East Africa and Madagascar. In China, a drug derived from *Illigera* is used widely to treat arthritis. *Gyrocarpus* has five species, of which one, *G. americanus*, is found in tropical coastal vegetation worldwide. *Sparattanthelium*, finally, occurs in the Guyana and Brazilian shield regions and the Amazon basin.

Atherospermataceae

The southern sassafras or Atherospermataceae are a family of trees and shrubs with two species in Chile and 12 in Australasia. Atherosperms are an important element of temperate forests of the Southern Hemisphere, where they are consistent ecological associates of the Southern Beeches (*Nothofagus*, Nothofagaceae)[link?]. Their wood, especially that of *Atherosperma moschatum* or Tasmanian sassafras is exploited commercially. The family is known from fossil wood and pollen from the Cretaceous of Antarctica.

Gomortegaceae

Gomortegaceae consist of single species in Chile, *Gomortega nitida*, a tree in danger of extinction because of overharvesting and anthropogenic forest fires. The family's earliest record is fossil wood from Late Oligocene-Early Miocene deposits in Chilean Patagonia.

Siparunaceae

Siparunaceae consist of two genera, *Glossocalyx* with one species in West Africa and *Siparuna* with about 65 species in the neotropics, mostly in the Andes. The family has no confirmed fossil record and no commercial interest.

Calycanthaceae

Calycanthaceae have three genera and eight species (Kubitzki, 1993b). *Calycanthus* (including *Sinocalycanthus*) comprises the frequently cultivated ornamental, Carolina allspice, *Calycanthus floridus*, the Californian allspice, *Calycanthus occidentalis*, and a Chinese species. *Chimonanthus* comprises four species in China of which Wintersweet, *Chimonanthus praecox*, is a widely cultivated ornamental. Finally *Idiospermum*, consists of one species in Queensland. This last species, first discovered in 1912 and morphologically very different from the other Calycanthaceae, is sometimes placed in a separate family, Idiospermaceae.

General characters and relationships of Laurales

Although molecular data have shown that the seven families described above descended from a common ancestor, no single morphological character is known that reliably distinguishes the order Laurales. Part of the reason for this may be that the Laurales diverged from their sister group, the Magnoliales, sometime in the Lower Cretaceous and have since lost their ancestral morphological characters. Two examples of this process are given below. Another reason may be that Laurales are predominantly tropical trees, the morphology, anatomy, and embryology of which is poorly known. A character seen in most Laurales is a well-developed floral cup, or cupule, that initially encloses the stamens and carpel (or numerous carpels) and later plays a role in seed-dispersal by supporting and displaying the single-seeded fruits. A phylogeny of the Laurales (Fig. 1 [emailed separately as a pdf file]) has Calycanthaceae as forming the first branch, followed by two clusters of families, Lauraceae, Monimiaceae, and Hernandiaceae, and atherosperms, *Gomortega*, and Siparunaceae (Renner, 1999). This phylogeny agrees with the distribution of several morphological characters. For example, Calycanthaceae have two ovules, while all other Laurales have solitary ovules. Lauraceae, Monimiaceae, and Hernandiaceae all have apical ovules, while Atherospermataceae, *Gomortega*, and Siparunaceae ancestrally had basal ovules, a condition lost in *Gomortega*. Calycanthaceae lack floral nectaries, while most other Laurales have paired nectar glands on the filaments. These glands were lost in Siparunaceae and in higher Monimiaceae concomitant with a change in pollinators away from nectar-foraging flies and bees to non-nectar feeding beetles and gall midges. Finally, most Laurales, except Calycanthaceae and Monimiaceae, have stamens with anthers dehiscing by two or four apically-hinged valves. Depending on the correct placement of a Calycanthaceae-like fossil flower (Friis *et al.*, 1994), valvate anther dehiscence, with the valves initially hinged laterally not apically, may be ancestral in Laurales and lost in modern Calycanthaceae and Monimiaceae.

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