

Moraceae of Papua

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Number of Genera and Species

THE 37 genera of Moraceae have a broad range of inflorescence forms, pollination syndromes, and breeding systems (Datwyler and Weiblen 2004). Most of the 1,100 species are figs (*Ficus*) known for a unique inflorescence and obligate pollination mutualism with fig wasps. In Papua, there are ten genera and 173 described species, dominated by *Ficus*, with 151 species, and followed by *Artocarpus*, with seven.

Distribution and Habitat

Moraceae are distributed from tropical to temperate forests throughout the world but the great majority of species are restricted to tropical rainforest. In New Guinea, the family occurs from the lowlands to cloud forest up to 2,400 m above sea level. *Ficus* is a prominent member of forest communities throughout the island in terms of local species richness and abundance (Weiblen 1998). About 70% of these species are endemic to the island and alpha diversity is extreme. In a lowland rainforest, for example, it is not uncommon to encounter up to 50 *Ficus* species within a few hundred hectares. Species turnover at a regional scale, on the other hand, appears to be quite low. In a comparison of four lowland rainforests across the Ramu and Sepik river basins, for instance, at least half of the *Ficus* species are shared between any two sites, even those separated by 500 km (G.D. Weiblen, unpublished data). The uneven density of collections across the island make it difficult to discern patterns of local endemism but most species appear to be widespread, perhaps related to dispersal by vertebrate frugivores (Dumont et al. 2004). Merely seven *Ficus* species (4%) appear to be limited to Papua, and only four (2%) to New Britain and the Bismarck Archipelago. The generally widespread distribution of *Ficus* species runs contrary to the biogeographic notion that mountainous New Guinea is an engine of plant speciation because of geographic isolation of populations. As we shall see, the mode of speciation in *Ficus* is likely related to the uniquely specialized mode of pollination (Weiblen and Bush 2002).

The fossil record and molecular divergence of Moraceae suggest that the family is at least 90 million years old and the distribution of tribes suggests either a Gondwanan or Laurasian origin (Datwyler and Weiblen 2004).

Family Classification

Molecular data indicate that Moraceae are part of the Rosidae and are closely allied to the Urticalean rosids, including Cannabaceae, Celtidaceae, Urticaceae,

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Cecropiaceae, and Ulmaceae (Sytsma et al. 2002). The Urticalean rosids differ from most other rosids in the presence of solitary ovules, laticifers, cystoliths, paired inflorescences in the leaf axils, and unisexual flowers. Urticaceae plus Cecropiaceae are sister to the Moraceae, distinguished from the latter in having laticifers only in the bark, clear latex, and orthotropous ovules (Sytsma et al. 2002).

Moraceae are divided into five tribes according to a recent phylogenetic classification of the family (Datwyler and Weiblen 2004). These are represented in New Guinea by the monotypic Ficeae, the Artocarpeae with *Artocarpus*, *Parartocarpus* (1 species) and *Prainea* (1), the Castilleae with *Antiaris* (1) and *Antiaropsis* (1), and the Moreae with *Fatua* (1), *Maclura* (3), *Streblus* (3), and *Trophis* (4). Paperbark mulberry (*Broussonetia*) is introduced.

Features of the Family

Habit includes trees, shrubs, hemiepiphytes, climbers and herbs. **Stipules** are present. **Leaves** are alternate, simple, entire to lobed to serrate, with milky latex in all parenchymatous tissue. **Inflorescences** distinguish the tribes. Ficeae are characterized by a syconium, an urn-shaped receptacle lined with flowers and enclosed at the apex by a ring of bracts. Plants are monoecious with bisexual inflorescences or gynodioecious but functionally dioecious (Weiblen 2000). Artocarpeae are dioecious or monoecious with unisexual inflorescences ranging from spikes to globes to solitary flowers. Castilleae are dioecious or monoecious with discoid to urceolate receptacles ringed by bracts. Moreae are dioecious to monoecious with relatively simple racemes, spikes or globose heads. **Flowers** are reduced and, when present, the perianth is 4- or 5-merous, tepaloid, and membranous. Filaments are either straight or inflexed in bud. Inflexed stamens in the Moreae are associated with a pistillode against which the anthers are appressed in bud. These stamens, springing outward at anthesis to release their pollen, are associated with wind pollination. The perianths of pistillate flowers are often fused to the receptacle, a condition hypothesized to protect the flowers against phytophagous insects (Berg 1990). **Fruits** are aggregates of drupes or achenes, often with a fleshy receptacle.

Gaps in Floristic Documentation or Knowledge

Probably the greatest turnover in floristic composition of Moraceae occurs across the altitudinal gradient from lowland forest to montane forest. However, the altitudinal limits of many *Ficus* species in particular are not well documented. There is a need to explore the species limits of montane versus lowland taxa, as well as patterns of intraspecific variation across the island, and species limits in the complexes of climbing figs (35 New Guinean species in subgenus *Synoecia*), and cauliflorous figs (50 New Guinean species in subgenus *Sycomorus*).

Natural History

Fig pollination is one of the best known examples of obligate mutualism between plants and insects, and was reviewed by Cook and Rasplus (2003). In general, the

associations between figs and their pollinators, microscopic wasps in the subfamily Agaoninae of parasitic Hymenoptera, are species-specific. It appears that each *Ficus* species in New Guinea is associated with a unique pollinating wasp species (Wiebes 1982). Female fig wasps actively or passively pollinate fig flowers while galling a fraction of fig ovaries. Each fig wasp larva feeds on and destroys a single developing ovule. The fate of ovaries as either seeds or galls depends on the intricate interactions between the style lengths of fig flowers and the ovipositor lengths of pollinators (Weiblen 2004). In monoecious fig species, seeds and wasps develop within each fig due to the presence of range of style lengths. In functionally dioecious species, seeds and wasps develop in different figs on separate plants (Weiblen et al. 2001). The pollination mutualism in New Guinea is also impacted by non-pollinating fig wasps, including gallers and parasitoids.

In contrast to the host-specific associations between *Ficus* species and their pollinator wasps, seed dispersal is accomplished through more generalized associations with vertebrate frugivores. Figs are eaten by birds, bats, and marsupial mammals in New Guinea, which mostly pass the seeds undamaged through their digestive systems, resulting in dispersal. Most ripe fig crops are visited by more than one animal species and different fig species may attract different guilds of animals (Shanahan et al. 2001). Feeding preferences appear to be influenced by traits including the position of the figs on the plant as well as fig color, size, and nutritional content. The distinctive geocarpic species that bear figs on leafless runners at or just below the soil surface appear to be dispersed by bandicoots, pigs, and rats. Cauliflorous trees are often visited by bats (Dumont et al. 2004), while the hemiepiphytic stranglers have axillary figs consumed by birds including cuckoo shrikes, birds of paradise, bowerbirds, pitohuis, hornbills, and parrots. The endemic Vulturine Parrot appears to be a particular specialist on the distinctive figs of section *Malvanthera*, where the seeds are embedded in a lignified endocarp and receptacle (Mack and Wright 1998).

The hemiepiphytic growth habit of figs in subgenus *Urostigma* (23 species in New Guinea) is also noteworthy. The seeds of all members in this group germinate in the forest canopy and become established as epiphytes, later sending aerial roots to the ground on the way to reproductive maturity. Some species strangle and kill their host tree to become free-standing trees with aerial roots while others remain entirely dependent on their hosts for structural support. This growth habit contrasts sharply with the climbing figs (subgenus *Synoecia*) which recruit from the forest understory and reach the canopy by means of adventitious roots adhering to host tree trunks.

Moraceae are also economically important in subsistence agriculture with *Ficus* playing a major role in forest regeneration following gardening. The edible leaves and fruits of secondary forest species including *F. copiosa*, *F. wassa*, and *F. dammaropsis* are used throughout New Guinea in traditional cooking. Wild and cultivated breadfruit (*Artocarpus camansi* and *A. altilis*, respectively) are an important source of starch in Melanesia. In addition, the fibrous bark of many arboresecent Moraceae is the source of tapa cloth. Boiled leaves of *Ficus pachyrrhachis* are used

to dye traditional grass skirts and the latex of many species, especially *Ficus septica* and *Maclura cochinchinensis*, is employed in traditional medicine.

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