Santalales (Mistletoe)

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Introductory article

Article Contents

Mistletoes are flowering plants in the sandalwood order (Santalales) that parasitize the branches of trees and shrubs. Mistletoes have evolved approximately five times in the order and are important in forest ecology, pathology and medicine.

Introduction

Among the various nutritional modes displayed by flowering plants, parasitism represents one of the most successful. This heterotrophic mode has evolved independently approximately ten times within angiosperms. One such group is Santalales, an order composed of six families that includes sandalwoods and mistletoes. Although all parasitic plants attach to their host via one or more haustoria, they can be further categorized as hemiparasites and holoparasites depending upon the degree of nutritional dependence upon the host. All members of Santalales are hemiparasites; however, some attach to host roots and others attach to host stems. Aerial (stem) parasites, generally called mistletoes, can be found in four families of Santalales: Loranthaceae, Misodendraceae, Santalaceae and Viscaceae (**Table 1**). All of these plants are obligate hemiparasites, meaning they require attachment to the host to complete their life cycle. Some of the more advanced mistletoes (e.g. *Arceuthobium*) approach holoparasitism, yet none have achieved this condition because photosynthesis is required during the seedling stage of development prior to host attachment.

Taxonomy and Phylogenetics

Molecular phylogenetic investigations have contributed new evidence to address relationships among members of the sandalwood order. From these data it appears that root parasitism evolved only once within 'Olacaceae', a paraphyletic assemblage that is traditionally classified as one family in Santalales (**Figure 1**). From such root parasitic ancestors, stem parasites evolved on at least four and possibly five separate occasions (**Figure 1**, clades 1–5). Thus, the term mistletoe refers to shrubby branch parasites that are not monophyletic (all sharing a common ancestor) but that have evolved independently in four families of Santalales (**Table 1**). All members of Misodendraceae and Viscaceae are mistletoes, but this is not the case for Loranthaceae and Santalaceae where root parasites can also be found. As shown in **Table 1**, the vast majority of mistletoe genera and species are found in Loranthaceae (74 of the 89 genera, 900 of the 1436 species). This family shows extensive diversification at the generic level, in contrast to

Table 1. Numbers of mistletoes

Clade	No. of genera	No. of species	Examples of genera
1. Misodendraceae	1	*c*. 8	*Misodendrum*
2. Loranthaceae[a]	74	*c*. 900	*Agelanthus, Amyema, Phthirusa, Psittacanthus, Scurrula, Struthanthus*
3. Santalaceae C[b]	3	11	*Antidaphne, Eubrachion, Lepidoceras*
4. Santalaceae D[c]	4	37	*Dendromyza, Dendrotrophe, Dufrenoya, Phacellaria*
5. Viscaceae	7	*c*. 480	*Arceuthobium, Dendrophthora, Ginalloa, Korthalsella, Notothixos, Phoradendron, Viscum*
Totals	89	*c*. 1436	

[a] *Atkinsonia, Gaiadendron* and *Nuytsia* are root parasites.
[b] Traditionally classified as Eremolepidaceae.
[c] Tribe Amphorogyneae in part.

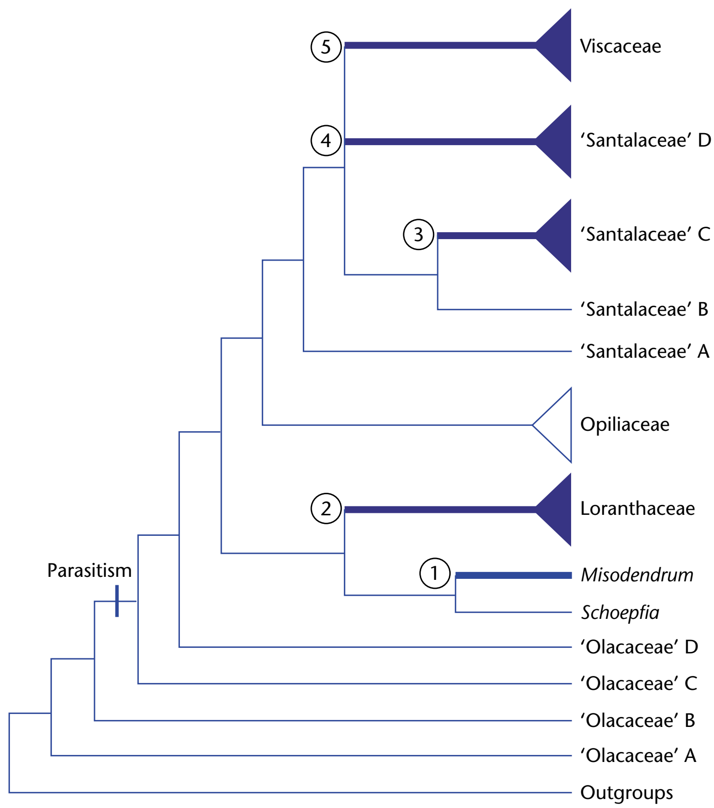

Figure 1 Generalized phylogenetic tree showing relationships among the component clades of Santalales (sandalwood order). Current evidence suggests that parasitism arose once in the order in clades C and D of Olacaceae. Branches above this point with thin lines are root parasites whereas those with thick lines represent mistletoes, a habit that has evolved independently approximately five times. This tree is derived from DNA sequences obtained from nuclear and chloroplast genes.

Viscaceae, which contains only seven genera but several hundred species. The majority of the 480 species of Viscaceae are attributed to only two genera: *Phoradendron* and *Viscum*.

The molecular tree shows that *Schoepfia* is not closely related to other Olacaceae but is sister to *Misodendrum*, the 'feathery mistletoes' that parasitize southern hemisphere beech trees (*Nothofagus*) in Chile and Argentina. This arrangement indicates that the common ancestor of *Misodendrum* and Loranthaceae was a root, not a stem parasite. Relevant to this discussion is the fact that three genera of Loranthaceae (*Atkinsonia*, *Gaiadendron* and *Nuytsia*) are root parasites and are thought to be the most primitive members of the family. If stem parasitism is a component of the definition of a mistletoe, then technically these three genera are not mistletoes. This demonstrates that the term mistletoe is, in one sense, taxonomic (because all are in Santalales) but in another sense is only a description of a particular habit found in several evolutionary lineages.

As with Olacaceae, 'Santalaceae' are paraphyletic. Of the 37 genera in this family, 30 are root parasites and the remaining seven are stem parasitic mistletoes. Molecular evidence indicates that these mistletoes evolved two times independently (**Figure 1**). One of these clades has traditionally been classified as Eremolepidaceae and the other represents a part of the tribe Amphorogyneae, which is otherwise composed of root parasites. The last group of mistletoes is Viscaceae, a strongly supported clade of seven genera.

Morphology, Life Cycle and Ecology

The morphological features of mistletoes are various depending upon which taxonomic group is being considered. Most members of Viscaceae have simple, somewhat brittle leaves with entire margins. These occur opposite on stems with constricted nodes. In some (e.g. *Arceuthobium*) the leaves are reduced to scales. The flowers are inconspicuous, monochlamydous and unisexual, forming spikes or cymes on monoecious or dioecious plants. In contrast, Loranthaceae generally have opposite or alternate leaves and large, brightly-coloured, dichlamydous, bisexual, flowers that display coadaptations to bird pollination. Older classifications often placed members of Viscaceae and Loranthaceae together within a broadly defined family. However, considerable evidence now exists to treat them as distinct groups (e.g. anther dehiscence, pollen shape, embryo sac development, and base chromosome number).

An important component of the life cycle of all mistletoes is the seed. Most mistletoe seeds are covered by a sticky substance called viscin that allows attachment to the host branch. Exceptions include *Nuytsia* with a winged seed and *Misodendrum* with a plumed seed, both of which are wind dispersed. Birds are the agent of dispersal for the seeds of many mistletoe species in Loranthaceae and Viscaceae. In the palaeotropics, seed dispersal involves spectacular coevolutionary adaptations with flower peckers (Dicaeidae). Seed dispersal is explosive in dwarf mistletoes (*Arceuthobium*) by means of hydrostatic pressure that builds up within the fruit. Seeds are discharged at 27 metres per second and may travel as far as 16 metres. Once attached to a host branch (by means of viscin), the mistletoe seed germinates and the primary root or hypocotyl forms the haustorium. In this phase of the life cycle, the seedling is particularly vulnerable to desiccation and must rapidly establish contact with the host xylem. Seedlings are also photosynthetic at this stage, from chlorophyllous endosperm and/or cotyledonary tissues. Host specificity is determined at the time of haustorial penetration. Some mistletoes exist at this early stage entirely within the host branch as an endophyte (e.g. *Arceuthobium*), whereas others (e.g. Loranthaceae) form more typical epicotyls, shoots and leaves. To move water from the host xylem to the parasite haustorium, mistletoes must produce a water potential more negative than their hosts and this is accomplished by higher transpiration rates. Pollination of mistletoe flowers may involve wind and insects (Viscaceae) or birds (Loranthaceae).

Biogeography and Fossil History of Mistletoes

Given the requirement that their seeds land on a suitable host, dispersability in Loranthaceae is limited. For this reason, and the scattered, continental distribution of relictual genera on austral landmasses, vicariance is the most likely biogeographical model to apply to this family. Vicariance assumes that ancestral Loranthaceae populations were separated by plate tectonic events that isolated the Gondwanan continents. Cytology also reflects the biogeographic history of the family. The primary base chromosome number for the family is 12, which occurs in *Atkinsonia* (eastern Australia), *Gaiadendron* (New World tropics), and *Nuytsia* (western Australia). By at least the early Cretaceous, Loranthaceae had already attained a high degree of differentiation. This is evidenced by the late Cretaceous pollen flora from Seymour Island, Antarctica, which contains Loranthaceae (*Cranwellia*) pollen as well as that from other tropical and cool temperate families. Following extensive rifting during the Tertiary, the loranth flora differentiated on the isolated island continent of Australia. By mid Miocene, the Australian plate collided with the Sunda island arc system, thus initiating an extensive exchange of Loranthaceae, both from Australia north and from Malesia south across Wallace's line.

In contrast to Loranthaceae, Viscaceae are thought to be a Laurasian group. Origins of five of the seven genera can be traced to eastern Asia. Moreover, the world distribution of the genera is not explained by vicariance but by range expansions that took place during the Tertiary. For example, progenitors of the entirely New World genera *Phoradendron* and *Dendrophthora* are thought to have migrated from Asia during this time. *Arceuthobium* is the only genus of mistletoe that occurs in both the Old and New World. The genus probably arrived in North America via a Bering land connection during the Miocene and then underwent extensive adaptive radiations on Pinaceae in both the USA and Mexico.

Importance of Mistletoes

In countries with traditions rooted in European culture, mistletoe is integrally linked with the Christmas holiday. The tradition of kissing under the mistletoe may be a relic of ancient druidic New Year ceremonies that associated this plant with fertility. In Europe, the holiday mistletoe is *Viscum* whereas in North America it is *Phoradendron*.

Viscaceae, particularly *Viscum album*, has been extensively examined for the presence of compounds (e.g. viscotoxins) that may have either toxic or therapeutic effects. Especially in northern Europe, mistletoe extracts have been used to combat cancer, despite some controversy over the efficacy of this practice. Mistletoe lectin (ML) appears to be the major biologically active component. It is a glycoprotein that is classified as a type II ribosome-inactivating protein owing to its ribosomal RNA-cleaving ability (similar to but less toxic than ricin). ML induces apoptosis in human cells by inhibition of protein synthesis.

Mistletoes are also important because of their negative impact upon commercially valuable trees. The dwarf mistletoes (*Arceuthobium*) are native components of forests of North America and Mexico yet they cause the loss of 11.3 million cubic metres of wood annually from the western US conifers (valued at several billion dollars). Mistletoes in Loranthaceae (e.g. *Amyema*, *Tapinanthus*, *Dendrophthoe*, *Phthirusa* and *Psittacanthus*) can also become problematic pathogens on ornamental and fruit trees.

Further Reading

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