

Santalales (Including Mistletoes)

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Mistletoes are flowering plants in the sandalwood order (Santalales) that parasitise tree branches. They evolved five separate times in the order and are today represented by 88 genera and nearly 1600 species. Loranthaceae (c. 1000 species) and Viscaceae (550 species) have the highest species diversity. In South America *Misodendrum* (a parasite of *Nothofagus*) is the first to have evolved the mistletoe habit ca. 80 million years ago. The family Amphorogynaceae is of interest because some of its members are transitional between root and stem parasites. Many mistletoes have developed mutualistic relationships with birds that act as both pollinators and seed dispersers. Although some mistletoes are serious pathogens of forest and commercial trees (e.g. *Arceuthobium*), the vast majority are benign and in some cases beneficial to humans (e.g. *Viscum album* for anticancer drugs). Mistletoes play important roles in many forest ecosystems and their loss results in decreases in faunal diversity, thus making them keystone species.

Introduction

Among the various nutritional modes displayed by flowering plants, parasitism represents one of the most successful. This heterotrophic mode has evolved independently 12 times within the angiosperms resulting in over 270 genera and 4400 species (Nickrent, 1997). Despite their occurrence in nearly all biomes worldwide, parasitism in plants is often neglected and only animal parasites considered. The largest group of parasitic plants is the sandalwood order (Santalales) which is composed of 19 families, 5 of which contain aerial parasites called mistletoes. All parasitic plants attach to their host via a modified root called the haustorium. The degree of nutritional dependence varies, however, ranging from hemiparasites

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Introductory article

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that produce some of their own sugars via photosynthesis to holoparasites that do not photosynthesise. Holoparasites are thus totally dependent on their host plant for nutrients. Up until recently, all members of Santalales were considered hemiparasites. Molecular phylogenetic analyses have shown that the holoparasite family Balanophoraceae is part of this order (Nickrent *et al.*, 2005; Barkman *et al.*, 2007), however, its relationship to other families is yet to be determined. **See also:** [Nutrient Acquisition, Assimilation and Utilization](#); [Parasitism: the Variety of Parasites](#)

The sandalwood order is of interest from the standpoint of the evolution of parasitism because three early diverging families (comprising 12 genera and 58 species) are autotrophic and nonparasitic. Hemiparasitic Santalales make up the bulk of the order with 148 genera and 2278 species. Of these, 60% of the genera and 70% of the species are mistletoes. According to a recent revised classification of Santalales (Nickrent *et al.*, 2010), mistletoes occur in five families: Misodendraceae, Loranthaceae, Santalaceae, Amphorogynaceae and Viscaceae (**Table 1** and **Figure 1**). All of these plants are obligate hemiparasites, meaning they require attachment to the host to complete their life cycle. Some mistletoes such as *Arceuthobium* and *Phacellaria* approach holoparasitism, yet none have achieved this condition, possibly because photosynthesis is required during the seedling stage of development before host attachment.

Taxonomy and Phylogenetics

Molecular phylogenetic investigations have contributed crucial evidence needed to address relationships among members of the sandalwood order. Mapping the incidences of root parasitism upon the phylogenetic tree (**Figure 2**), it appears that this trophic mode evolved only once within the order. From such root parasitic ancestors, stem parasites evolved on five separate occasions (Vidal-Russell and Nickrent, 2008a). Thus, the term mistletoe refers to shrubby branch parasites that do not all share a common ancestor (thus, are not monophyletic) but that have evolved independently in five different families of Santalales. All members of Misodendraceae and Viscaceae are mistletoes, but stem and root parasites are found

Table 1 Numbers of mistletoes

Family	Number of genera	Number of species	Examples of genera
1. Misodendraceae	1	10	<i>Misodendrum</i>
2. Loranthaceae ^a	73	990	<i>Agelanthus</i> , <i>Amyema</i> , <i>Phthirusa</i> , <i>Psittacanthus</i> , <i>Scurrula</i> , <i>Struthanthus</i>
3. Santalaceae ^b	3	11	<i>Antidaphne</i> , <i>Eubrachion</i> , <i>Lepidoceras</i>
4. Amphorogynaceae ^c	4	37	<i>Dendromyza</i> , <i>Dendrotrophe</i> , <i>Dufrenoya</i> , <i>Phacellaria</i>
5. Viscaceae	7	550	<i>Arceuthobium</i> , <i>Dendrophthora</i> , <i>Ginalloa</i> , <i>Korthalsella</i> , <i>Notothixos</i> , <i>Phoradendron</i> , <i>Viscum</i>
Totals	88	1598	

^a*Atkinsonia*, *Gaiadendron* and *Nuytsia*, while in Loranthaceae, are root parasites.

^bTraditionally classified as Eremolepidaceae.

^cTraditionally considered part of Santalaceae; here also includes dendroparasites.

in Loranthaceae, Santalaceae and Amphorogynaceae. As shown in **Table 1**, the vast majority of mistletoe genera and species are found in Loranthaceae (70 of the 88 genera, 987 of the 1598 species). This family shows extensive diversification at the generic level, in contrast to Viscaceae, which contains only seven genera but several hundred species. The majority of the 550 species of Viscaceae are attributed to only two genera: *Phoradendron* and *Viscum*.

Traditional classifications of Santalales (Cronquist, 1988) generally incorporated a broad concept for Olacaceae and Santalaceae. The tree shown in **Figure 2** is based on several multigene molecular phylogenies (Der and Nickrent, 2008; Malécot and Nickrent, 2008; Vidal-Russell and Nickrent, 2008a, b), thus it is taken as the best representation of the organismal phylogeny. Current classifications strive to name clades, that is monophyletic groups. Based on past classifications, the following families were all considered Olacaceae: Erythropalaceae, Strombosiaceae, Coulaceae, Ximeniaceae, Aptandraceae, Olacaceae (strict sense), Octoknemaceae and Schoepfiaceae. The tree topology shows that this 'family' is paraphyletic. Similarly, past classifications considered these families to be 'Santalaceae': Comandraceae, Thesiaceae, Cervantesiaceae, Nanodeaceae, Santalaceae (strict sense), Amphorogynaceae, also a paraphyletic assemblage. To rectify this problem, the Angiosperm Phylogeny Group (APG III, 2009) lumped Viscaceae into a broadly defined Santalaceae. The opposite approach was taken by Nickrent *et al.* (2010), that is to split Olacaceae and Santalaceae into several families. This new concept resulted in monophyletic, strongly supported families that are now more easily diagnosed, as opposed to other classifications where these families included plants with a confusing array of morphological diversity.

The phylogenetic tree (**Figure 2**) shows that the first clade to evolve the mistletoe habit involves Misodendraceae and Loranthaceae. A study that incorporated fossil data to calibrate the molecular tree with time (Vidal-Russell and

Nickrent, 2008a) showed that the first mistletoes were ancestors of Misodendraceae, a lineage that evolved approximately 80 million years before present (mybp). *Misodendrum*, called the 'feathery mistletoes' based on their wind-dispersed fruits, parasitises southern hemisphere beech trees (*Nothofagus*) in Chile and Argentina (Vidal-Russell and Nickrent, 2007a). These mistletoes share an ancestor with Schoepfiaceae, a family of root parasitic trees, shrubs and herbs. The pattern of an aerial parasite clade evolving from a root parasitic ancestor is repeated in the remaining mistletoe clades. For Loranthaceae, the lineage dates to the Cretaceous with early diverging root parasitic clades emerging *c.* 45 mybp. Stem parasitism in the loranthids is a more recent innovation, dating to *c.* 30 mybp. In Santalaceae, a group of mistletoes, formerly recognised as family Eremolepidaceae, evolved in the neotropics *c.* 53 mybp.

One of the most fascinating clades to evolve the mistletoe habit is Amphorogynaceae (**Figure 3**). Within this family are plants with a wide range of parasitic habits (Der and Nickrent, 2008). These include root parasites (*Amphorogyne*, *Choretrum* and *Leptomeria*), mistletoes (*Dufrenoya* and *Phacellaria*), stem parasitic lianas (called dendroparasites, e.g. *Dendromyza*) and amphiphagous parasites (*Daenikera* and *Dendrotrophe*). The latter condition, describing plants that attach to roots, stems or both simultaneously, is of interest because it may represent a transitional mode between root and stem parasitism. When three parasitic modes (root, stem and dendroparasite) are optimised on a fully resolved molecular tree, the ancestral condition for the family appears to be equivocal, which is equivalent to amphiphagous (**Figure 2** and **Figure 3**). This suggests that the common ancestor of Amphorogyneae and Viscaceae was amphiphagous. Whether this was the actual trophic mode of the ancestor is unknown, but the result suggests that genetic plasticity existed early in the history of the highly successful mistletoe family Viscaceae. Older classifications often placed members of Viscaceae and Loranthaceae



Figure 1 Representatives of the five mistletoe clades. (a) *Misodendrum brachystachyum* (Misodendraceae), female plant with plumose, wind-dispersed fruits (Photo courtesy of L Kelly). (b) *Amyema celebica* (Loranthaceae), inflorescences with showy, bird-pollinated flowers (photo taken in the Philippines by D Nickrent). (c) *Lepidoceras chilense* (Santalaceae), fruiting plant (photo taken in Chile by G Amico); (d) *Dendromyza ledermannii* (Amphorogynaceae), a twining dendroparasite with young male flowers; inset shows closer view of fruits from a female plant (photos taken in Papua New Guinea by D Nickrent). (e) *Phoradendron serotinum* (Viscaceae), female plant with inflorescences (top of shoots) bearing tiny, insect-pollinated flowers and bird-dispersed fruits (below) (photo taken in Illinois, USA by D Nickrent).

together within a broadly defined family; however, molecular phylogenetic (Figure 2) and other sources of evidence (Calder, 1983) strongly support treating them as distinct families.

Morphology, Life Cycle and Ecology

The morphological features of mistletoes are various depending on 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 *Arceuthobium* and some species of *Phoradendron* and *Viscum*, 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 have alternate, opposite or whorled leaves. The flowers of loranth, arranged in many different inflorescence types, are generally bisexual and dichlamydous, although the calyx is reduced and called a calyculus. Flowers with small, greenish, white or yellow petals are adapted to insect pollination, whereas those with large, brightly coloured flowers are coadapted to bird pollination. In the palaeotropics, the flower peckers (family Dicaeidae), sun-birds (Nectariniidae) and honeyeaters (Melphagidae) are highly adapted to feeding on mistletoe nectar and this is accompanied by specific behaviours associated with pollination. Bird pollination in the neotropics is mainly performed by hummingbirds (Trochilidae). Wind pollination has been documented in some Viscaceae, although insects may also be involved.

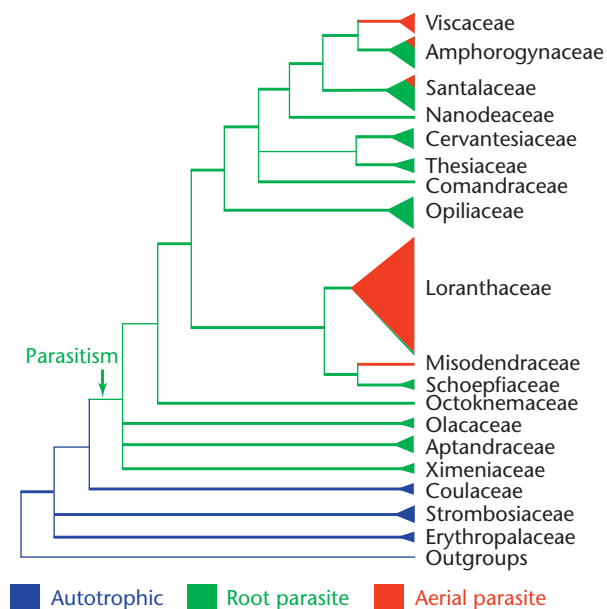


Figure 2 Generalised phylogenetic tree showing relationships among the component clades of Santalales (sandalwood order) based on Nickrent *et al.* (2010). This tree is derived from deoxyribonucleic acid (DNA) sequences obtained from nuclear and chloroplast genes. Current evidence indicates that parasitism arose once in the order. Thick branches indicate a high degree of support for that clade. Adapted with permission from Nickrent *et al.* (2010).

Another 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 most mistletoe species, the exception being the dwarf mistletoes (*Arceuthobium*, Viscaceae) whose seeds are dispersed explosively by means of hydrostatic pressure that builds up within the fruit. Discharged seeds travel at 27 m/s and may land 16 m away. In the palaeotropics, mistletoe seed dispersal involves spectacular coevolutionary adaptations with flower peckers (Dicaeidae). After ingestion the seed is passed through the entire digestive system in less than 25 min. The sticky seed attaches to the host branch by its viscin and then germination ensues. The hypocotyl forms the haustorium, an organ that affects the physiological and morphological link to the host. The young seedling is particularly vulnerable to desiccation and must rapidly establish contact with the host xylem. Seedlings are also photosynthetic at this stage, producing their own food from chlorophyllous endosperm or cotyledonary tissues. After haustorial penetration, the mistletoe may grow entirely within the host branch as an endophyte (e.g. *Arceuthobium*), or it may form more typical epicotyls, shoots and leaves (e.g. Loranthaceae). 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. The

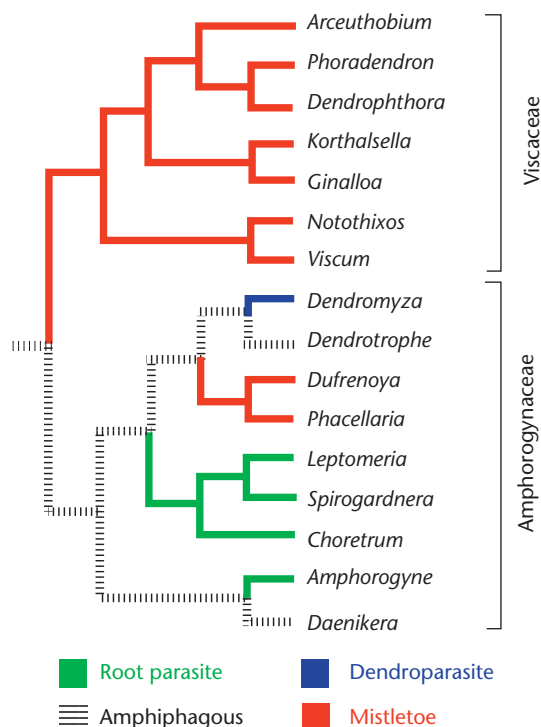


Figure 3 Phylogenetic tree showing relationships among genera in Amphorogynaceae and Viscaceae (from Der and Nickrent, 2008). The character states 'stem', 'root' and 'dendroparasite' were optimised on the tree using MacClade 4 (Maddison and Maddison, 2000) which resulted in the backbone of the tree being reconstructed as equivocal, here equated with amphiphagy, that is attaching to either roots, stems or both.

evolution of epiparasitism, where one mistletoe is an obligate parasite on another mistletoe, is a remarkable physiological adaptation because the second member of the association must have a very negative water potential. **See also:** Ecology of Water Relations in Plants; Plant–Water Relations; Roots and Root Systems

Biogeography of Mistletoes

Plant biogeographers are interested in knowing the history of how particular species have attained their present distribution. Two basic processes are typically considered: vicariance and dispersal. Vicariance involves an ancestral population that is fragmented by environmental events (e.g. mountain building, continental drift). In contrast, a new plant population may become established from an ancestral one via a dispersal event. Subsequent to vicariance and dispersal, the resulting subpopulation diverges from the ancestral population developing greater genetic differences over evolutionary time.

Until recently, the main biogeographic hypothesis explaining the current worldwide distribution of Loranthaceae mistletoes involved vicariance (Barlow, 1990). This explanation seemed feasible because dispersal of

loranth seeds is limited given their requirement for a suitable host. Moreover, two root parasitic, Australian genera with the primary base chromosome number for the family of $X=12$ (*Atkinsonia* and *Nuytsia*) were considered relictual, that is left isolated on one of the fragments of the original Gondwanan supercontinent. Karyotypic differentiation (aneuploid chromosome number reduction to $X=8, 9, 10$ and 11) and speciation was assumed to have taken place on the periphery of Gondwana during the late Cretaceous. These new taxa, isolated by continental drift, underwent radiations in Malaysia, Australia, South America and Africa producing the current worldwide distribution of loranth on southern continents.

Up-to-date information on the positions and timings of southern continent separations, as well as a time-calibrated molecular phylogeny of Loranthaceae, shows that Barlow's hypothesis is only partially true. Although Loranthaceae originated on Gondwana, in the late Cretaceous, Africa and India had long since separated from Antarctica (162 mybp) and South America (135 mybp). Thus, Loranthaceae present in those areas today could not have gotten there via vicariance. Moreover, dispersal has apparently played a greater role than vicariance in loranth biogeography (Vidal-Russell and Nickrent, 2007b).

The following seems to be the most likely scenario explaining current loranth distribution. A root parasitic loranth ancestor spread from Antarctica to southern South America, Australia and New Zealand when these areas were still contiguous (late Cretaceous to Palaeocene, 80–60 mybp). Ancestors of present day *Gaiadendron* and *Atkinsonia* subsequently evolved in South America and Australia, respectively (Oligocene, *c.* 30 mybp). The first stem parasitic loranth evolved soon after and spread widely in Antarctica, Australia and New Zealand. The success of stem parasitic mistletoes may be correlated with development of temperate deciduous woodlands and savannas in the Oligocene. By this time, all loranth became extinct in Antarctica because it was ice covered. The Australian plate collided with the Sunda volcanic arc system in the mid Miocene, thus generating a migration avenue between Australia, New Guinea and southeast Asia. Some New Zealand loranth underwent an aneuploid reduction ($X=12$ to 11), and by mid-Miocene they migrated stepping stone fashion along emerged islands of the Lord Howe Rise or the Norfolk Ridge, eventually reaching New Caledonia and New Guinea. Later this lineage experienced another aneuploid reduction ($X=11$ to 9). These $X=9$ ancestral loranth entered Papuasias, as did a separate clade of mistletoes originating in northern Australia. Later in the Miocene, both the $X=9$ and 12 clades of loranth had spread into Indomalaya and Asia and gave rise to numerous extant genera. These lineages spread and diversified in Indomalaya and Papuasias, some becoming 'intrusive' and crossing back over Wallace's line into Australia. The $X=9$ lineage dispersed widely reaching Africa in the Miocene. There an explosive adaptive radiation occurred, mainly owing to the development of savannah habitats. Both sunbirds and flowerpeckers diversified and spread from

Australia into Asia and Africa in the Miocene, thus setting the stage for co-evolution between mistletoes and their pollinators/seed dispersers. **See also:** [Biogeographical Regions](#)

In contrast to Loranthaceae that are Gondwanan, Viscaceae are thought to be a Laurasian group diverging from Amphorogynaceae *c.* 72 mybp. Five of the seven genera are exclusively Asian and only *Arceuthobium* has species in both the Old and New World. A recent study sequenced the conserved inverted repeat region of the chloroplast genome of Old and New World *Arceuthobium* which showed that the latter are most similar to *Phoradendron* (Nickrent and García, 2009). Because *Phoradendron* (and its close relative *Dendrophthora*) comprises entirely New World mistletoes, the most likely scenario is that it shared a common ancestor with *Arceuthobium* that occurred in that hemisphere. Supporting this idea is the fact that both *Arceuthobium* and *Phoradendron* are most diverse in the highlands of Mexico. Previously it was proposed that *Arceuthobium* originated in the Old World and arrived in North America via a Bering land connection during the Miocene (Hawksworth and Wiens, 1996). The molecular data suggest that the migration took place in the opposite direction.

Importance of Mistletoes

In countries with traditions rooted in European culture, mistletoe is integrally linked with the Christmas holiday (Tainter, 2002). 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 treat a number of diseases such as diabetes, epilepsy, hepatitis and cancer (Büssing, 2000). For cancer therapy, 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 ribonucleic acid (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 (Mathiasen *et al.*, 2008). 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. In general, the vast majority of mistletoes are not pathogens and indeed many serve as important components of natural ecosystems. Even dwarf mistletoes

that are considered pathogens because they deform conifer host branches (form witches' brooms) play a role as a native forest component. Several birds and mammals use witches' brooms as nesting sites (Mathiasen *et al.*, 2008). Mistletoes also provide a food resource to frugivorous birds. Experiments in Australia (Watson, 2001) demonstrated that sites where mistletoes were artificially removed showed a significant decrease in bird diversity. Thus, mistletoes may act as keystone species, that is species that are not dominant by numbers or biomass but that have a disproportionately high influence on the entire ecosystem. **See also:** [Coevolution: Host–Parasite](#); [Forestry Management and Production](#)

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