

THE BIOGEOGRAPHIC HISTORY OF LORANTHACEAE

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Loranthaceae, with 73 genera and ca. 900 species, comprises mostly aerial hemiparasites, but three monotypic genera are entirely root parasitic. The family occurs mainly in tropical areas worldwide, although they are also found in temperate habitats of Europe, Asia, South America, Australia and New Zealand. As seen in all members of tribes Nuytsiae and Elytrantheae, the base chromosome number for the family of $x = 12$. As a result of aneuploid reduction, subtribe Loranthinae has a haploid chromosome number of nine and subtribe Psittacanthinae of eight. In a recent phylogenetic analysis of the family that included 60 genera (Vidal-Russell, 2007), the three root parasites were supported as successive sister taxa to a clade composed of the remaining aerially parasitic genera.

Based on the distribution of relict genera found in south temperate regions, Barlow (1983, 1990) hypothesized that by the late Cretaceous Loranthaceae had a wide distribution in Gondwana. Moreover, following the breakup of the supercontinent, major radiations occurred in Malaysia, Australia and South America. Different genomic basal stocks were proposed: Afro-Indian, Indian-Indoasian, Australasian-Papuanian and South American. Barlow proposed that these four evolutionary lines were isolated by the fragmentation of the supercontinent. The objective of this study is to use present day distributions of genera and molecular phylogenetic data to reconstruct the historical biogeography of the family.

The worldwide distribution of Loranthaceae was divided into seven geographical areas: Africa, South America, Asia, Malaysia east of Wallace's line (New Guinea), Malaysia west of Wallace's line, Australia and New Zealand. A matrix for 36 genera with one multistate character (areas) was built and optimized on a phylogenetic tree using MacClade (Maddison & Maddison, 2000). This tree derived from a Bayesian analysis of a 5-gene

matrix containing SSU and LSU nuclear rDNA, *matpK*, *rbcL* and *trnL-F*. Divergence-vicariance analysis was also performed using DIVA (Ronquist, 1996).

The character optimization and DIVA analyses suggested that the family was widespread in Gondwana (Australia, New Zealand, South America and New Guinea). Today, three taxa survive that represent that early assemblage of root parasites: Nuytsia, Atkinsonia and Gaiaedendron. When New Zealand started rifting around 80 mya, a vicariance event (Fig. 1, no. 1) left two ancestors: the first being Clade A (subtribe Elytrantheae) in New Zealand, which speciated and later dispersed into Asia and Australia, and the second composed of the remaining loranthids. This second clade, which could be called "Prototupeia", was probably widespread in Australia, Antarctica and South America. A second vicariance event around 35 mya (Fig. 1, no. 2) separated "Prototupeia" into South American and Australian lineages, the latter accompanied by an aneuploid reduction to $x = 11$. The survivors of the South American lineage are today represented by *Desmaria*, *Ligaria*, *Notanthera*, and *Tristerix* that further differentiated into tribe Psittacanthinae with $X=8$ (Clade B). The support for the *Tupeia* / *Desmaria* clade is weak, thus it cannot be determined at present whether *Tupeia* derives from the Australian or South American lineages. A member of the Australian lineage dispersed to New Zealand, with subsequent speciation resulting in *Muellerina* (Australia) and *Ileostylus* (New Zealand). Dispersal of the *Muellerina*/*Ileostylus* ancestor into Asia was accompanied by another aneuploid reduction to $X=9$. This migration likely took place via the Lord Howe Rise to New Caledonia, eventually reaching New Guinea. Further dispersal and differentiation resulted in the *Amyema* complex of Malaysia. Ancestral loranthids continued migration through Asia to

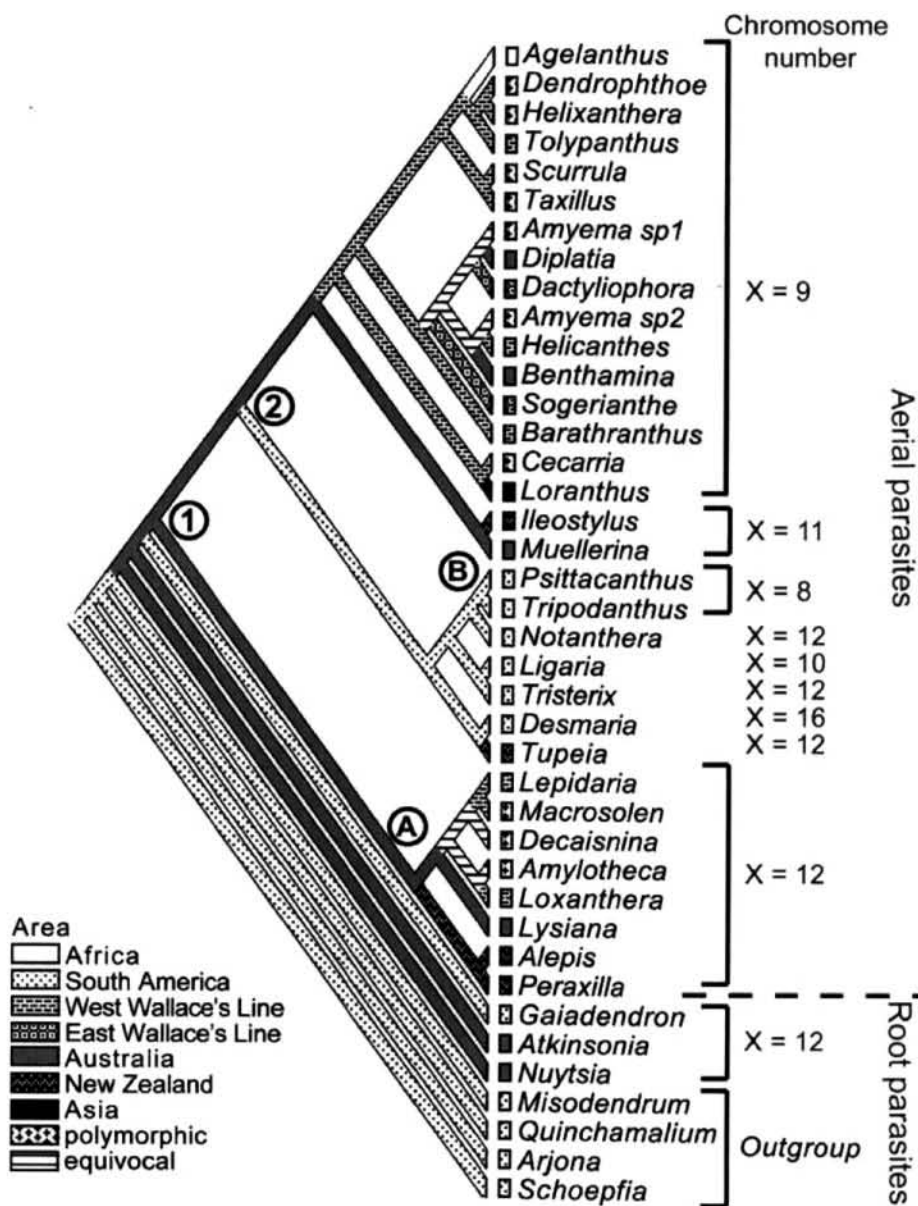


Fig. 1. Area optimization on a molecular tree resulting from a matrix of small-subunit (SSU) and large-subunit (LSU) nuclear rDNA, matK, rbcL and trnL-F. Ancestral areas were reconstructed under the parsimony criterion and via a dispersal-vicariance analysis. Numbers within circles indicate proposed vicariance events. Clades discussed in the text are labeled A and B. The African clade is represented by only one taxon: *Agelanthus*.

the Middle East and eventually Africa where a massive adaptive radiation produced the African clade. These events were reinforced by coevolution with mistletoe birds (families Nectariniinae and Dicaeidae) that currently pollinate and disper-

se Loranthaceae in these areas. After the collision of the Australian plate with the Sunda Island Arc system 15 mya, major exchanges occurred between these areas allowing more derived genera such as *Amyema*, *Dendrophthoe*, and *Benthamina* to

migrate into Australia. This exchange may have been driven by the only species of *Dicaeum* found in Australia, which is estimated to have migrated into Australia in the Pliocene (Reid, 1988).

Our findings agree only in part with Barlow's biogeographic hypotheses. We agree that the family originated in Gondwana during the late Cretaceous, but importantly this is long after the separation of Africa and India. Africa separated from Antarctica around 162 mya and from South America 135 mya (McLoughlin, 2001). Because these dates are prior to the possible origin of Loranthaceae (ca. 90 mya according to molecular dating and the earliest authentic loranth fossil at ca. 83 mya), we hypothesize that Loranthaceae was absent from Africa when it separated from Gondwana. Similarly, it appears that Loranthaceae were also absent from India because it rifted north from Antarctica-Australia ca. 130 mya, colliding with Asia ca. 43 mya (McLoughlin, 2001). On these points, our data conflict with Barlow's hypotheses as to how Loranthaceae reached Africa and Asia. By reconciling molecular phylogenetic tree topologies with existing tectonic and paleobotani-

cal data, our understanding of the biogeography of Loranthaceae, a fascinating Gondwanan plant family, has been advanced.

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