attempting to measure the tensile strength of very long nanotubes.

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Switch from specialized to generalized pollination

The once prevalent view that the evolution of extreme ecological specialization is accompanied by a loss of potential for adapting to new conditions, and thus is irreversible[1-4], has been challenged by several recent examples[1,2,5]. However, we know of no modern phylogenetic studies showing reversal in pollination relationships from extreme specialization to generalization, although such reversals are theoretically expected[6,7]. Here we present molecular phylogenetic evidence for an evolutionary shift in *Dalechampia* (Euphorbiaceae) vines from a highly specialized relationship (pollination by one or a few animal species[2,7]) with resin-collecting bees to generalized pollination by a variety of pollen-feeding insects. This shift was associated with dispersal from Africa to Madagascar, where the specific resin-collecting pollinators are absent. These results show that plants dispersing beyond the range of their specific pollinators may succeed by evolving more generalized pollination systems.

Only a few genera of bees in the families Megachilidae and Apidae use floral resin in nest construction[8,9], and only two genera of plants, *Dalechampia* and *Clusia* (Clusiaceae), are known to secrete resins that attract pollinators[8]. Partly because the reward they offer is non-nutritive, *Dalechampia* blossoms that secrete resin are pollinated by only one or two species of bees at any one location, and so depend on specific pollinators. In eastern and southern Africa, for example, *Dalechampia* populations are usually pollinated by only one species of *Pachyanthidium* or *Heriades* (Megachilidae)[9,10]. Recent fieldwork in Madagascar has shown that the species of *Dalechampia* found there offer only pollen as a reward for pollinators, and that most are pollinated by a variety of pollen-feeding insects, including beetles (Cerambycidae, Scarabidae), muscoid flies (Diptera) and several bees (Halictidae, Anthophoridae, Apidae). Open presentation of a common food reward (pollen) results in interactions with numerous pollinators[10], a finding typical of plants with open flowers[6].

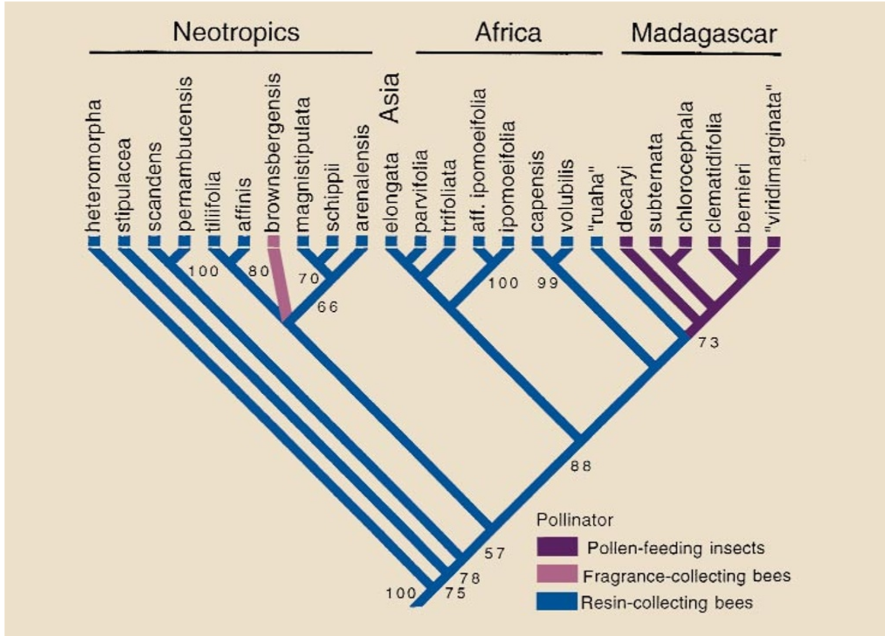

Figure 1 A phylogenetic hypothesis for *Dalechampia* sects. *Dalechampia* and *Tiliifoliae* based on maximum parsimony (MP) analysis of combined nuclear ribosomal (ITS-1, 5,8S, ITS-2) and chloroplast (*trn*K intron) DNA sequences. The strict consensus of MP trees is depicted, with bootstrap values (above 50%) along branches. The tree shown is part of a larger tree from an analysis including 16 representatives of the other sections of *Dalechampia* and two species from candidate sister genera (*Plukenetia* and *Tragia*). Evolution of pollination ecology was mapped using MP onto the tree based on the observed pollination of each species. The species are endemic to the regions indicated except *D. parvifolia*, which occurs in both Africa and Asia.

Phylogenetic analysis of combined nuclear ribosomal and chloroplast DNA data sets, and mapping of pollination and morphological traits onto the molecular tree, indicate that Malagasy species of *Dalechampia* are descended from an ancestor pollinated by resin-collecting bees (Fig. 1). These results also indicate that *Dalechampia* colonized Madagascar from Africa (Fig. 1). This finding is further supported by morphological data and biogeographical considerations[10].

But why did the Malagasy colonists 'abandon' efficient, specialized pollination by resin-collecting bees and switch to a generalized pollination system? It seems that resin-collecting megachilid bees, which are the only pollinators of *Dalechampia* in Africa[9], failed to colonize Madagascar[10]. The ancestral *Dalechampia* colonists of Madagascar were probably pollinated incidentally by other pollen-feeding insects. They subsequently adapted to the absence of their specific pollinators by losing the gland that secretes the resin reward and by effectively using diverse pollen-feeding insects as pollinators. These changes were sufficiently successful to allow secondary diversification on the isolated island of Madagascar.

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