Balsaminaceae in Southeast Asia: systematics, evolution, and pollination biology

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SUMMARY

Balsaminaceae, or the 'Balsams', is a family of flowering plants, which is characterized by an herbaceous growth form and mostly bilateral symmetrical or asymmetrical flowers with spurred lower sepals and explosively dehiscent fruits. The family consists of one species of *Hydrocera* and more than 1000 species of *Impatiens*, and is mainly distributed in tropical Africa, Madagascar, southern India and Sri Lanka, the Sino-Himalayan region, and Southeast Asia. In this thesis, I present new findings on the taxonomy, systematics, pollination biology, and evolution of Balsaminaceae, specifically focussing on Southeast Asian taxa. The first part of my thesis emphasises the diversity of Balsaminaceae in Myanmar.

Sixty-six species of this family were found in Myanmar with new records for 20 species. In addition, four new species were described: *Impatiens tanintharyiensis*, *I. decurva*, *I. oblongata* and *I. hartnolliae*. An identification key to the different species and a description of the morphology, phenology, ecology and distribution range of each species are presented. Balsams are distributed almost all over Myanmar, although they are mainly concentrated in montane areas with few taxa distributed in the lowlands. Most species are terrestrial or lithophytic. To improve the classification of the genus *Impatiens*, DNA sequences of almost one fifth of the family were used to examine the morphological evolution of the genus and compare it to previous classifications. From that study, it became clear that previously used characters that were used to define section *Semeiocardium* need to be reconsidered. The presence of connate lateral united petals is a diagnostic character of this group, and a clade with free lateral united petaled flowers that includes *I. stenosepala* should be separated from this section.

To understand the association between floral variation and pollination systems, I observed seven co-occurring balsams in the Chiang Dao Wildlife Sanctuary for two months. I observed that a species with small, spurless flowers, and without nectar is characterized by autonomous self-pollination. The species with short spurs and large floral chambers with a wide entrance to the flower are bee-pollinated. The species with long spurs and a small floral chamber with a narrow entrance are bimodally bee- and lepidopteran-pollinated. Among bee-pollinated species, two species have asymmetrical corollas, which results in highly specific pollen placement on a specific part of the bee's body, namely the left-hand side of the upper thorax as well as the left-hand side of the bee's wing, and the right legs of the bee, respectively. There are no significant differences in nectar

volume among the animal-pollinated species. To understand the evolution of floral morphology related to pollination systems, the phylogeny and the ancestral state of the pollination system and corolla symmetry was reconstructed for a large number of Asian species. The different pollination systems within *Impatiens* can be categorised according to floral morphology, consistent with the results of my pollination studies. However, on a global scale, spurless small-flowered species can also be fly-pollinated in some cases, and in Africa, species with red flowers and a large floral entrance and short spur are bird-pollinated.

The reconstruction of the evolution of character states revealed that bee-pollination is ancestral in balsams. However, the ancestral state of floral symmetry could not been confirmed. The pollination system shifted around forty times: from bees to bimodal (bees and Lepidoptera), from bimodal to bees, from bees to autogamy or flies, from bimodal to autogamy or flies and from bimodal to birds, respectively. These shifts in pollination system were mainly present in *Impatiens* section *Uniflorae*, which includes many species from Africa, Madagascar, and Asia. Corolla symmetry shifted between bilateral symmetry and asymmetry around twenty times. In contrast to the shifts among pollination systems, the shifts in floral symmetry were concentrated in other clades, including species that are ancestrally bee-pollinated and mainly distributed in Asia. I concluded that pollinator-driven evolution in *Impatiens* occurs according to two processes: pollination system shifts and divergent use of the same pollinator. The pollination system shifts are mostly associated with colonisation to new areas where bumblebees (the ancestral pollinator) are absent, while the floral symmetry shifts occur in areas where bumblebees are abundant, and competition for pollinators may be strong.

In future, to understand the diversity of Balsaminaceae in continental Southeast Asia, a taxonomic revision of the family in other Asian countries, such as Cambodia, Laos and Vietnam, is needed. In addition, the infrageneric classification of *Impatiens* needs further improvement. Some of the sections are in need of redelimitation, which could be achieved by combining molecular phylogenetic analyses with morphological analyses. In order to better understand the effect of pollination shifts on the evolution of the genus, it will be necessary to focus on selected species and areas for field studies. The application of methods, such as single-visit experiments, should be considered to assess the relative importance of multiple pollinators in species with bimodal pollination systems.