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Evolutionary Trends in Pollination Syndromes of Neotropical *Gesneriaceae*

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Fossil pollen or macrofossils of the Gesneriads have not yet been discovered at all. The oldest pollen record for the closest herbaceous relatives of *Gesneriaceae* in the *Scrophulariales* date between the lower Miocene to the Pliocene (22.5–5 Mio), which implies that *Gesneriaceae* are probably not older than that. Indeed this family is among the latest to evolve within the angiosperms, even later than the *Asteraceae* (WIEHLER 1982). The center of diversity of Neotropical *Gesneriaceae* lies in the mid-elevation Andes of Colombia and Ecuador. This orobiome began to develop with the rise of the Andes, which started about 12 Mio years ago and is still ongoing. The diversity center of Gesneriads matches well with that of Trochilidae (hummingbirds), the most important pollinators (60%) of Gesneriads . The earliest remains of hummingbirds date back to the lower Oligocene (34–23 Mio., MAYR 2005). Modern Chiroptera are even older and fossil records were found in the Eocene (50 Mio.). The origin of flying insects dates back into the carboniferous (350 Mio.). So far it is not possible to date when insects actually started to pollinate flowers, but it is likely that their coevolution with flowering plants began, when these plants occurred, probably at least during the Cretaceous (145–65 Mio.).

Anyhow, we can conclude that at the time of the Gesneriad occurrence, all their modern pollinator groups already existed in a wide range of taxa. Nectar-feeding bees were probably among the first pollinators (gynandro-euglossinophily, 30% of all taxa). Other insect pollination syndromes include psychophily, sphinghophily, phalaenophily, myiophily and andro-euglossinophily (perfume collecting male bees), but these account for less than 8%. Most variations in flower morphology are found in ornithophilous and chiropterophilous groups. This variability sometimes

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makes it rather difficult to define species limits, e.g. in some *Dalbergaria* species [*D. picta* (KARSTEN) WIEHLER] or *Capanea* species (*C. grandiflora*), leading to a considerable high amount of misplacements and synonyms. It is therefore suggested that ornithophily and chiropterophily evolved from insect-pollinated groups, especially gynandro-euglossinophily.

Other remarkable features are the „hybrid-pollination-syndromes" found in some taxa: it is not obvious whether hummingbirds or bats are the legitimate pollinators – maybe even both? Field observations are urgently needed to focus on this phenomenon. The following sympatric taxa show hybrid-pollination morphology and would be good objects to start with:

- *Capanea grandiflora* DECAISNE has a wide corolla opening, is completely creme colored with dark dots and anthesis at night and has no odor. Only bats were observed to pollinate. *Capanea hansteinii* FRITSCH however has a narrower corolla opening, only the front part of the corolla has creme colored petals with dark dots, but the corolla limb is pinkish-red, anthesis is both, diurnal and nocturnal, no odor: hummingbirds were observed to pollinate, but bats as pollinators can not be excluded.
- *Kohleria bogotensis* FRITSCH: morphology and coloring is like *C. hansteinii*, but the limb diameter is smaller than that of the close related *K. amablis* (PLANCH. & LINDEN) FRITSCH, whose base color of the front corolla part is pink.
- *Gloxinia purpurascens* (RUSBY)WIEHLER: natural variations as well as plants under cultivation sometimes do have a purple and sometimes a green corolla entrance part.
- *Gasteranthus pansamalanus* (DONN.SMITH) WIEHLER has a hypocyrtoid bright orange corolla and is ornithophilous, *G. aurantiacus* (FREIBERG 2000) has a funnel shape bright orange corolla and is ornithophilous as well, but the rather close related *G. leopardus* (FREIBERG 1996) has a funnel shape yellow corolla with brown markings and perfume hairs and is pollinated by male Euglossine bees looking for and gathering perfume.

Some of these hybrid features have also been shown in *Sinningieae* (SANMARTIN-GAJARDO & SAZIMA 2005).

The hybrids between chiropterophily and ornithophily suggest that the evolution of both syndromes is very close, but the directions are not obvious. The author hypothesizes that the morphology of Gesneriads gives some clues to decide which direction is the most probable, but extensive field studies are needed to verify these.

The following features exclusively target hummingbirds for additional attraction:

- extrafloral pollinator attraction: parts of leaf undersides (tips, rims, main veins etc.) are predominantly red and glow when penetrated by light („church-window-effect").

- Species with long tubular flowers increase there front size appearance and thus visibility by adding infrapetal appendages in the purely ornithophilous genus *Trichantha*.
- The hypocyrtoid flower form evolved independently in many different genera, e.g. *Gasteranthus, Alloplectus, Besleria, Drymonia, Nematanthus, Neomortonia, Paradrymonia, Parakohleria*.
- In addition to regular nectar, some taxa offer sticky slime kept by the sepals [e.g. *Drymonia coccinea* (AUBL.) WIEHLER].

In summary, there are much more special adaptations to ornithophily than to chiropterophily in Gesneridas, which leads to the assumption that the still ongoing trend in rapid evolution for these taxa is from ornithophily to chiropterophily.

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