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ORCHID POLLINATION: RECENT DEVELOPMENTS FROM BRAZIL

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Because of their remarkable flower morphology, orchids are particularly interesting objects of study. Most orchid species hold their pollen in discrete packs, so-called pollinia (singular; pollinium). These pollinia, together with other pollinium stalks, form more or less complex translatory units, so-called pollinaria (singular: pollinarium). During their visits to the flowers, orchid pollinators dislodge these pollinaria and deposit their pollen content during successive flower visits. Pollinators may be attracted to the flowers in many ways. Many orchids offer flower parts or secretions (nectar, trichomes, wax-like or resin-like compounds, aromatic compounds, oils, etc.) that can be gathered/foraged by their pollinators. Yet, many orchids "deceive" their pollinators and offer no flower reward. Many orchids are merely "food-frauds", displaying a set of flower features (colors, fragrances) that apparently elicit the attraction of food-seeking animals. A much more sophisticated kind of deception involves the so-called "pseudocopulation". In this kind of pollination strategy, flower features (mainly flower fragrance, but also coloration and – when applicable - indument or pilosity) mimic these of some female insects (mostly Hymenoptera). Pollination is achieved when male insects attempt copulation with these "dummy females".

Since the times of Darwin, the pollination biology of the orchids has received the attention of both, lay persons and scientists. The combination of their remarkable flower structure plus their often bizarre pollination strategies has played a major role in the understanding of evolution, morphology and pollination biology as a whole.

Orchid pollination studies in the Neotropics experienced a boost in the sixties (Van der Pijl & Dodson 1966, and literature therein) with the understanding of Euglossini behaviour. The males of these bees gather fragrances (aromatics, terpenes, sesquiterpenes, etc.) at specialized parts of the lip of many orchid species from different neotropical subtribes (specially Catasetinae, Stanhopeinae and some Zygopetalinae) and perform the pollination during successive flower visits. The reasons why Euglossini males collect these compounds are still a matter of speculation (see Singer & Koehler 2003 for a brief discussion of the theories). Yet, it is possible that these compounds are somehow used during courtship. In the last six years, a number of contributions on orchid pollination have been made by Brazilian or Brazilian-based researchers. The purpose of this contribution is to give a brief review of these papers and to communicate some – in my opinion - remarkable findings which are part of ongoing projects. I have chosen to describe the findings by taxonomic groups.

Subfamily Orchidoideae (including Spiranthoideae, sensu Dressler 1993). Studied species in this subfamily have been shown to be self-compatible, but pollinator-dependent. Automatic self-pollination – when present - is associated with rostellum narrowing, thus the stigmatic secretion passively contacts the pollinia. Bee pollination was recorded for some species of the genera of the so-called "*Pelexia* alliance" (Spiranthinae: *Cyclopogon, Pelexia* and *Sarcoglottis*) (Singer & Sazima 1999). Hummingbird pollination was demonstrated in *Stenorrhynchos lanceolatum* (Spiranthinae) (fig. 1B) (Singer & Sazima 2000). Moth pollination and protandry was recorded in *Sauroglossum elatum* (Spiranthinae) (Singer 2002b) and *Prescottia stachyodes* (Prescottiinae) (Singer & Sazima 2001b). Bee and moth pollination, in absence of protandry has been recorded in *Prescottia densiflora* and *P. rodeiensis*, respectively (Singer & Cocucci 1999, Singer & Sazima 2001b). Bee pollination was recorded in two Goodyeriinae orchids: the protandrous *Erythrodes arietina* and the non-protandrous *Aspidogyne longicornu* (Singer & Sazima 2001a). Mixed moth and crane-fly (Tipulidae) pollination was documented in *Habenaria parviflora* (Habenariinae) (fig. 1A) (Singer 2001). Protandry was traditionally associated with Bumble-bee pollination. Now, it is clear that this flower feature appears in orchids with other kinds of flower vectors. Since protandry in Orchidoideae has been recorded in species of the closely related subtribes Goodyeriinae, Spiranthinae and Prescottiinae, it has been suggested that this flower feature arose early in the tribe Cranichideae (where the aforementioned subtribes belong) and was lost many times, independently (Singer 2002b).

Subtribe Pleurothallidinae: Pollination by Calliphorid flies was recorded in *Pleurothallis luteola*, from Southern Brazil (Singer & Cocucci 1999c). More recently, Borba & Semir (2001) and Borba *et al.* (2001) described with great detail the pollination biology and breeding system of several rupicolous *Pleurothallis* species from southeastern and northeastern Brazil. The pollinators of these orchids are quite specific and these plants apparently perform inbreeding depression.

Subtribe Sobraliinae: Ongoing research has shown that at least *Elleanthus brasiliensis* is protandrous (fig. 1C-D). To my knowledge, protandry is herein reported for the first time in subtribe Sobraliinae. I have briefly observed the hermit *Phaethornis petrei* (Trochilidae: Phaethorninae) pollinating this orchid in southeastern Brazil. Yet, this orchid may be pollinated by many different hummingbirds, as additional observations will surely reveal. In Colombia, María Argenis Bonilla (UNAL) and her students have also observed several hummingbird species pollinating some Andean *Elleanthus* spp. (A. Bonilla, pers. comm.). Preliminary evidence indicates that *E. brasiliensis* is self-compatible, but pollinator-dependent.

Subtribe Bulbophyllinae: Borba & Semir (1999) and Borba *et al.* (1999) have described in detail fly-pollination in several rupicolous *Bulbophyllum* species from southeastern Brazil. In these orchid species, pollination is wind-assisted. The lip is hinged to the base of the lip and vibrates with the slightest breeze. The fly pollinator adequately positioned in the lip surface is pushed against the column and adheres the pollinarium on the scutellum. In order to be deposited on the stigmatic surface, the pollinia have to dehydrate considerably (Borba & Semir 1999), a fact that prevents self-pollination.

Subtribe Angraecinae: *Campylocentrum aromaticum*, from southern Brazil was recorded as mainly bee-pollinated (mostly by Halictidae bees) (fig 1E). Yet, a few bug and fly species are able to dislodge pollinaria and, perhaps, can act as accessory pollinators (Singer & Cocucci 1999a). Meliponini bees were recorded as the pollinators of the leafless *Campylocentrum burchellii* (Singer & Cocucci 1999a).

Subtribe Maxillariinae: Meliponini bees of the genus *Trigona* were recorded as the pollinators of the rewardless, honey-scented *Maxillaria picta* flowers in southern Brazil (Singer & Cocucci 1999b). Further observations have confirmed that *Trigona* bees are also the pollinators of several other bifoliate Maxillarias of the '*Maxillaria picta*' complex (fig. 1F). *Trigona* bees have also been recorded as pollinators of *Maxillaria brasiliensis*. The bees dislodge and deposit the pollinaria while gathering portions of the wax-like lip callum (actually made-up by many tightly packed laminar, unicellular trichomes) (Singer 2002). Pollination through "pseudocopulation" mediated by *Plebeia* (Meliponini) drones was recently demonstrated for *Trigonidium obtusum* (Singer 2002a) (fig. 1G). Cultivated plants of the nectar-secreting *Maxillaria parviflora* have been observed being pollinated by small Meliponini bees and Ponerinae ants as well (R. B. Singer, unpublished) (fig. 1H).

Subtribe Oncidiinae: In the past, it was postulated that many "*Oncidium*" species (here used in its wider sense) were mimics of Malpighiaceous plants (Van der Pijl & Dodson 1966). It was postulated that these species of Malpighiaceae offered nectar and the pollinators of Oncidiinae orchids pollinated these flowers by mistake. So, plants and pollinators should be involved in mimicry complexes (Van der Pijl & Dodson 1966). However, there is increasing evidence that both, Malpighiaceae plants and many Oncidiinae orchids produce oils, which are gathered by females of several bee genera of family Apidae (these genera were formerly included in the no longer accepted family Antophoridae) (Singer & Cocucci 1999b, Reis *et al.* 2000 and literature therein). Therefore, it seems safer to assume that both, orchids and Malpighiaceae are part of a guild of plants pollinated by these oil-gathering bees, rather than pieces of a mimicry complex.

Pollination by oil-collecting *Tetrapedia* bees was documented for *Oncidium paranaense* (Singer & Cocucci 1999b). A female of *Tetrapedia* was captured when pollinating flowers of *Oncidium pubes* (R. B. Singer, unpublished). The bee dislodged a pollinarium when collecting the oil secreted in a superficial, lamellar elaiophore, at the lip surface. Vespidae wasps were recorded as the pollinators of *Capanemia thereziae* (Singer & Cocucci 1999b). The wasps adhere and deposit pollinaria while licking nectar secreted in a shallow nectary, on the surface of the lip.

Recently (Singer & Koehler 2003), some aspects of

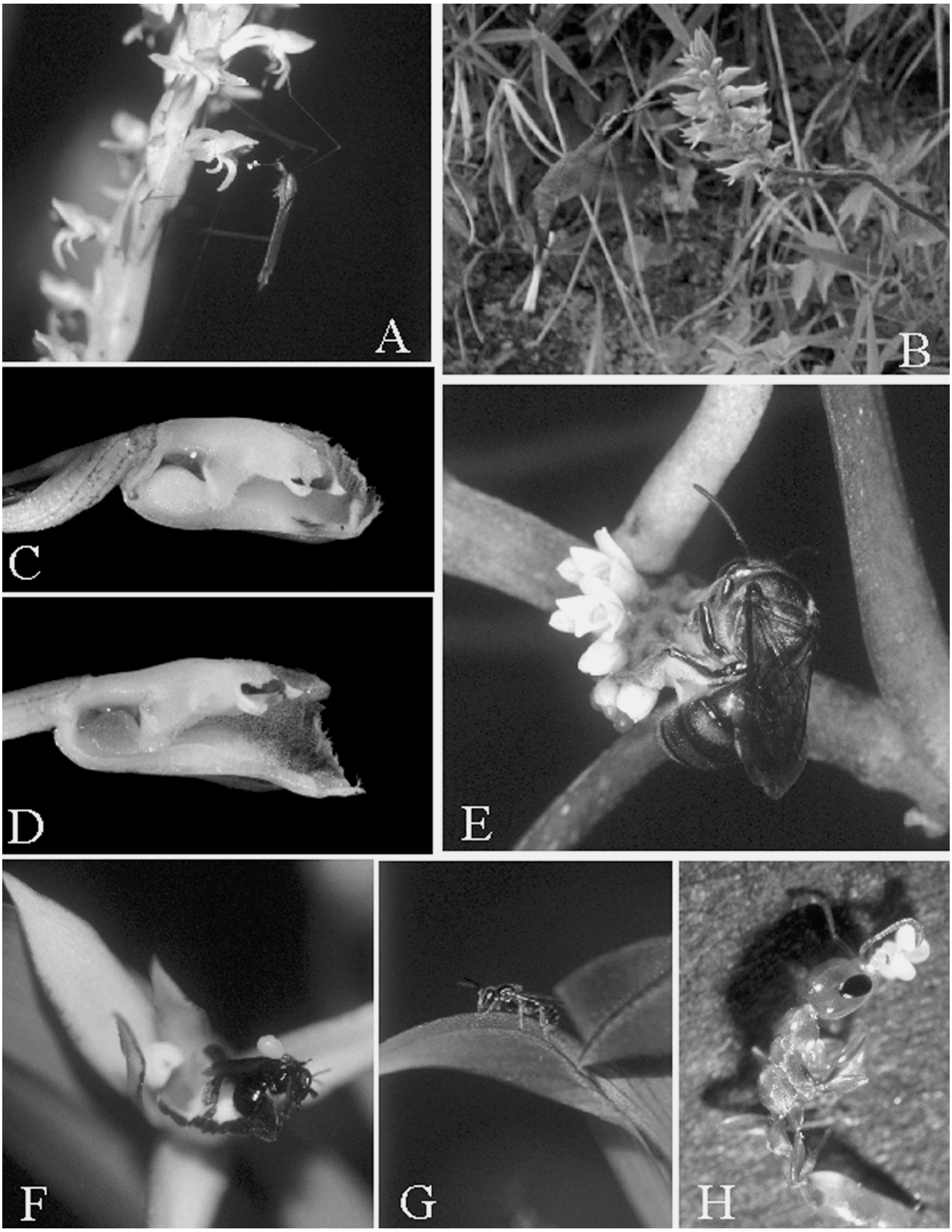

Figure 1. A. *Habenaria parviflora* (Orchidoideae: Habenariinae) being pollinated by a Tipulidae crane-fly. B. *Phaethornis eurynome* (Trochilidae) pollinating *Stenorrhynchos lanceolatum* (Orchidoideae: Spiranthinae). C-D. Protandry in *Elleanthus brasiliensis* (Sobraliinae). C: Male phase. D: Female phase. Notice the different column position in the two phases. E. *Campylocentrum aromaticum* (Angraecinae) being pollinated by a sweat-bee (Halictidae). F. *Trigona* (Meliponini) worker dislodging a pollinarium of *Maxillaria marginata* (Maxillariinae). G. *Plebeia* (Meliponini) drone attempting copulation with the dorsal sepal of *Trigonidium obtusum* (Maxillariinae). H. Ponerinae ant with a pollinarium of *Maxillaria parviflora* on its head.

the pollination of *Notylia nemorosa* have been highlighted. This orchid is protandrous and mostly self-incompatible. Pollinators are males of *Eulaema* and *Euglossa* that gather aromatic compounds at the lip surface. These bees tend to visit all available flowers in each inflorescence, a behavior that promotes some degree of geitonogamy (and abortion), since flowers in male and female phase may coexist in the inflorescence. It was suggested that the combination of self-incompatibility and this kind of pollinator behavior may be responsible for the rarity of fruits in several rewarding neotropical Orchidaceae (Singer & Koehler 2003).

With the advent of molecular tools, a new era has started for orchid pollination studies. It is hoped that once robust phylogenies are available, the evolution of some pollination-related traits could be traced and plotted in the cladograms. Thus, researchers could obtain reliable scenarios for the evolution of breeding systems and flower features. For instance, if we consider "protandry" as a character, it is clear that it evolved many times within Orchidaceae. Yet, a closer analysis indicates that (for example), the protandry of *Mormodes* (Catasetinae) is not comparable with that of the Cranichideae orchids. Oils are now known to occur in many Oncidiinae orchids. Still, these oils may be qualitatively different in different Oncidiinae groups (Reis et al. 2000). Briefing, it is hoped that a re-evaluation of pollination-related characters and their phylogenetic significance will happen. If so, exciting times may be going to come.

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