GENERALIST FLOWERS SYMPOSIUM

The generalist flower deconstructed

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At the XVIIth International Botanical Congress in Vienna, Austria (July 2005), we held a symposium entitled “Generalist flowers: their evolution, biology and animal associations”. By happy coincidence, this year also marked the 80th birthday of Professor Dr. Stefan Vogel, a 20th century pioneer in floral morphology and biology. Stefan Vogel, who makes his home near Vienna, graciously allowed us to dedicate our symposium in honor of his eightieth birthday. Professor Vogel still goes regularly to work at the Institute of Botany, Vienna, and like all true field botanists, eagerly into the field whenever possible. Indeed, it was in Cartagena, Colombia (on the occasion of the VIIIth Latin American Botanical Congress, 2002), that the first author had the pleasure of making his acquaintance. Carrying his Olympus stereo dissecting microscope in his suitcase and lens in hand, we explored coastal dry forest remnants not far from Santa Marta, in 40°C temperatures, revisiting an area he hadn’t been to for 50 years. We then mounted the Andes to visit a reserve near Villa de Leyva, reuniting us with Gerhard Gottsberger. Not entirely prepared for the cold, we wrapped ourselves in blankets, and Stefan set-up his microscope and camera so that he could study and photograph the flowers collected during the day (Fig. 1). His laser eye rarely missed sighting an interesting flower as we walked along and his encyclopedic knowledge of natural history greatly enriched our experience.

The beauty of natural history is that it provides a harmonious, immediate, readily understandable and realistic explanation of phenomena. It operates on a human level, which is the most practical one. Atomistic approaches see the parts (smaller and smaller divisions) with great acuity but often loose sight of the whole. Too atomistic a view can lead to the comparing of points and not systems (functional

Fig. 1. Stefan Vogel photographing a bat-pollinated *Kohleria tigridia* (Gesneriaceae) flower (Colombia, 2002).

wholes). By the same token, picking apart of phenomena (pattern) followed by painstaking reconstruction is not inherently the most efficient way to progress in the understanding of nature. There are many arguments (not the least being pragmatic) in favor of the use of "fuzzy logic", which takes general trends at face value and works from there. Philosophically, natural history, that is descriptive biology, is a sophisticated form of naive realism, and when combined with a modern understanding of mathematics, physics, chemistry, biochemistry, and developmental biology, is a very powerful approach for gaining insight into the basis and integrality of natural systems.

The papers presented in this symposium differed in the way pattern was perceived, analyzed and interpreted, but overall, represented a happy medium between holistic and atomistic reasoning. This is partly due to the topic "generalist flowers", which by its very nature implies many connections, obliging the student to look at the whole as well as the pieces. One paper, "Generalized *versus* specialized pollination modes in tropical floras: the case of the cerrado vegetation in Brazil" by Gerhard Gottsberger and Ilse Silberbauer-Gottsberger, given at the Congress is not included here because the substance of it has since been published in *Life in the Cerrado: a South American Tropical Seasonal Ecosystem*, vol. 2, by the same authors (see *Taxon* 56: 631–633 for a review).

Stefan Vogel opens the series of papers by giving us a glimpse of his personal aspirations and experiences within a historical context. A festschrift in his honor has been recently published in *Flora* and the interested reader is directed there for a more in-depth biography of this fascinating biologist as well as a complete list of his publications to 2005 (Weber & Sontag, 2006). Professor Vogel's contribution is followed by Labandeira, Kvaček and Mostovski's paleo-entomological and -botanical look at gymnospermous pollination systems. Now long-defunct gymnosperms and insects are resurrected and scrutinized, the more we look, the clearer it is that gymnosperms had complex and diverse entomophilous reproductive systems. Rather the way palms and extant cycads were once mistakenly thought to be strictly wind-pollinated, Mesozoic gymnosperms, too, are proving to be largely entomophilous, foreshadowing the pollination systems of angiosperms. As recognized by Whitehouse (1950), Faegri & van der Pijl (1971) and others, the prevalence of dioecy in gymnosperms (and rarity of co-sexuality) was probably to assure out-crossing in plants having no, or at most a rudimentary, self-incompatibility system. Enclosure of ovules in a carpel went hand-in-hand with the development of efficient self-recognition filters and in this way reproductive system and population dynamics became revolutionized (Whitehouse, 1950).

The Middle to Late Cretaceous was a time of great upheaval and many plants, such as the Bennettitales, which had flourished in wide-spread communities since the Middle Triassic discovered the limits of their bauplan. Plants with more efficient and enticing physiological and reproductive systems co-opted the *functional guilds* of more ancient plants and their animal complements. Taking this line of reasoning a step further, we can see that just because the direct ancestors of certain insect lineages such as the Allocorynina, a recent group (Marvaldi & al., 2006) could not have been the original pollinators of such ancient plants as cycads does not preclude entomophily in Triassic and Jurassic cycads, insects of a similar functional group may have fulfilled the task. The following paper by Ødegaard and Frame, on phytophageous beetle visitors to flowers of two unrelated neotropical trees, brings this point home, as they conclude among other things that functional types (guilds) in small- to medium-sized flower visiting beetles remain relatively stable but that species change. There is an universality to their three functional groups, which they classified as "general flower visitors" (here largely pollen feeders), ovi-depositors in buds and flowers, and seed predators. These same three beetle functional types characterize cycads, palms and other predominately beetle floral systems and are symptomatic of the transcendence of guilds but not necessarily vertical lineages.

The next paper in the symposium, by Stefan Vogel's fellow student under Wilhelm Troll, Focko Weberling, elucidates the classical morphological (and typological) view of botany. Whatever the basal-most divergent extant angiosperm may be, and this will change with evolving criteria, the morphological "type" will be resilient in the same way as functional groups. Weberling presents his case for the most "primitive" flower type, which he contends is most similar to *Drimys* s.str. (Winteraceae). Another recurring issue in this series of contributions is that the former favorite model of ancient angiosperm flowers, *Magnolia stellata*, is in fact rather specialized. Weberling remarks on this, as does Ollerton, Killick, Lamborn, Watts, and Whiston in the paper after his. In temperate zones, small- to medium-sized beetles are pollinators of *Magnolia* species. As the climate warms up further south, heat-loving, large *Cyclocephala* (Dynastinae) beetles make their appearance and the typical Dynastinae (Scarabaeidae) large-beetle floral syndrome, well-known from many *Annona* species (and others), kicks in … leaving us wondering whether those large flowers in the cool north temperate zone were once visited by Scarabaeidae in former warmer times, thereby accounting for their gigantism and other peculiarities of their floral biology. Perhaps the *Magnolia* flower was the basic paradigm by default—it was a convenient answer—readily available to instructors and students in North America and Europe, it exhibited in widescreen Panavision what we wanted to see in a "primitive" angiosperm, in those days of temperate tunnel vision. Had our reference point been the tropical America's, *Drimys* might well have been the consensual basic form.

The subsequent paper in the series, Ollerton, Killick, Lamborn, Watts, and Whiston explains how modern pollination ecologists view generalist flowers and through their lens we learn to distinguish when we are comparing apples and apples, or apples and oranges, that is, ecological, functional and phenotypical generalization. That different floral biologists arrive at different answers has *everything* to do with using different definitions and posing different questions. Their approach to floral biology combines observation with experiment and tries to test the contribution of the various components of their defined ecosystem.

Working largely from the available literature and following a different tack, the final paper by Olesen, Dupont, Ehlers, and Hansen focuses on floral ecomorphology and pollination networks and attempts to identify the top-ten most generalized flowers. The authors begin by taking stock of their territory and speak of the historical awareness of tension between typology and evolution. We learn that to use the first does not negate a belief in the second; typology is a tool, a mnemonic device, not the international standard "meter" made of platinum-iridium alloy. They provide us with yet another definition of generalist flowers, this time explicitly linked to visitor functional groups. Sadly, too little is known of "total" networks and next to nothing about tropical lowland rainforests, which is why information from this ecosystem is missing from their dataset. They find, contrary to expectations, that there is no correlation between flower openness and relative generalization level and that tubular flowers achieve the highest generalization level, attributable to the great diversity of lepidopterans and bees in their surveyed systems. We should mention though that lepidopterans are usually of lesser numeric importance among visitors to flowers of rainforest canopy trees; canopy trees are not simply temperate herbs seen from another scale, as they appear to us from airplanes. To reach, remain and move around in canopy space poses many biotic and abiotic difficulties, which only certain animals solve given their bauplans—most notably among flower-visiting insects: coleopterans, dipterans, hymenopterans, and thysanopterans. The authors note that their results depend upon several factors such as how blossoms are classified and suggest that if a positive correlation between flower openness and high relative generalization level exists, it might be found *within* rather than among blossom classes. And fine differences are the stuff that generalization is made on …

We hope you enjoy and profit from the following papers as together we unfold the petals of that elusive entity, the Generalist Flower.

Literature cited

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