

WHAT DARWIN FORGOT TO MENTION ABOUT ORCHIDS¹

CARLOS M. HERRERA

*Estación Biológica de Doñana, Consejo Superior de Investigaciones Científicas, Apartado 1056, E-41080 Sevilla, Spain
E-mail: herrera@ebd.csic.es*

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It has been frequently highlighted (e.g., Ghiselin 1984) that the first of Darwin's books presenting detailed supporting evidence for the theory of natural selection after *The Origin* was his very carefully crafted treatise on orchids. There, he strived to gather evidence that, quite often, morphological traits of orchids were well suited for insect pollinators removing and depositing pollinia. But it has also been remarked that "what Darwin did not do was to explain how orchid flowers come to be different" (Wilson and Thomson 1996, p. 88). Ever since Darwin's time, attempts at elucidating the processes and mechanisms involved in the extraordinary diversification of angiosperm flowers, for which orchids represent the unquestioned epitome, have figured prominently in the research program of plant biologists. Animal pollinators have been quite often implied in explanations of angiosperm diversification, for at least the following good reasons: among animal-pollinated lineages, taxonomically distinctive traits are predominantly reproductive (Grant 1949); a suggestive temporal match exists, in geological time, between the radiations of angiosperms and several groups of animal pollinators (Grimaldi 1999); and there is compelling evidence that the radiation has been more rapid in lineages of animal-pollinated plants (Dodd et al. 1999).

There seems no question that, for immobile adult plants, enlisting the service of animals in predictably circulating male gametes between anthers and pistils of conspecific individuals represented a decisive evolutionary breakthrough. Thus, at the core of plant-animal pollination systems are, on one side, the ability of flowering individuals to advertise themselves and, on the other, the ability of animals to receive, manage, interpret, and remember the range of visual (flower colors and shapes) and chemical (floral scents) signals being "broadcast" by plants to identify themselves and inform prospective floral visitors about their spatial location and possible rewards. Animal pollination is, therefore, an essentially communication-based phenomenon, with plants as the signal producers and animals as the receivers. This is why the cognitive aspects involved in pollination may provide some critical hints to the still elusive problem of angiosperm diversification and, more specifically, to the actual role played by animal pollinators in the process. This possibility, however, has been so far hindered by the factual divorce between predominantly behaviorally and plant-oriented research practices. Evolutionary plant ecologists interested in

pollination biology have traditionally tended to seek adaptive explanations for plant or pollinator traits, with little knowledge of the neural mechanisms underlying the behavior of pollinators. Physiologists and neuroethologists, on the other hand, have tended to focus preferentially on the mechanisms by which environmental stimuli (plant signals) provoke or modify behavior, and have assumed almost automatically that the mere existence of a trait is sufficient evidence for its adaptive value. Chittka and Thomson's declared purpose in *Cognitive Ecology of Pollination* was to bridge the gap between these two separate traditions in the study of pollinators and plant pollination. This book clearly succeeds in identifying and putting together many of the different sorts of bricks needed to setup the bridge but also, and perhaps more importantly, in revealing how much bricklaying work needs still to be done to complete the structure.

Cognitive Ecology of Pollination is a collection of sixteen chapters spanning a remarkably diverse set of topics revolving around the plant-pollinator interface. By recruiting chapter authors from the ranks of behavioral ecologists, animal neuroethologists, insect physiologists, and a few "phyto-centric" (if somewhat unorthodox) pollination ecologists, the book provides a rich and multifaceted view of behavioral and physiological mechanisms involved in plant-pollinator interactions. The consequence is that the level of internal heterogeneity of the book is well above the average for edited multi-authored works of its sort. On the animal side, chapter topics include behavioral and neural mechanisms of learning and memory, vision, olfaction, choice behavior, and the subjective evaluation of stimuli, and an interesting and thought-provoking exploration of the basis and consequences of individual variation in pollinator behavior. On the plant side, we find chapters on frequency-dependent selection, assortative mating, pollen dispersal, and plant speciation. Although the diversity of topics and approaches was the natural consequence of the editors' well-reasoned intent to bring together quite diverse perspectives, some of the internal heterogeneity of the book is somewhat distracting and possibly superfluous. Some chapters, even though presenting interesting information and thought-provoking ideas, seemed to me a bit misplaced in a book having cognitive ecology as its central theme. These include Winter and von Helversen's chapter focusing on the foraging energetics of bat pollinators, and Dukas' imaginative (although with precious little empirical support) account of the potential ecological and evolutionary significance of predation on pollinators. Given the presumably stringent limits on book length set by the publisher, even a slight reduction in the number of chapters would have had the desirable consequence of allowing more room for

¹ *Cognitive Ecology of Pollination: Animal Behavior and Floral Evolution*. L. Chittka and J. D. Thomson, eds. 2001. Cambridge University Press, Cambridge, U.K. xiii + 344 pp. HB \$95.00, ISBN 0-521-78195-7.

deeper treatments of some particularly important and germane topics.

As expected from the book's title, the animal side of the plant-pollinator interface receives the most thorough coverage, with most chapters focusing on the sensory, behavioral, and cognitive aspects of animals that visit flowers (to be honest, and to my disappointment, just a tiny fraction of such animals, as the stage is occupied almost exclusively by bumblebees and honeybees; I will return below to this taxonomic bias). The book's subtitle, *Animal Behavior and Floral Evolution*, makes one expect recurrent forays into the subject of floral evolution. Nevertheless, and even though the *potential* evolutionary implications to plants of the cognitive aspects described are often evident, most of the animal-oriented authors either neglect to mention them or evince flagrant naïveté or uncritical pan-selectionism. With only a few exceptions, therefore, most of the animal-oriented chapters will arouse little enthusiasm among evolutionarily minded plant biologists. The editors themselves seem well aware of this problem, for they candidly comment in the preface on some "physiologists 'rounding up' a paper's discussion by adding a paragraph on the adaptive significance of the traits they describe" p. xi. An example is provided by the sweeping sentence closing Giurfa and Lehrer's chapter on honeybee vision and floral displays: "Natural flowers display exactly those parameters that bees tend to prefer." (p. 79) (Which flowers, which floral parameters, which bees? any field biologist might ask, acquainted with the extraordinary diversity exhibited by any of these three entities in nature.) That "sensory ecology needs to become more evolutionary" was recently emphasized in Chittka and Briscoe's (2001) title.

With the exception of a chapter devoted to spatial learning in hummingbirds, most of the chapters in this book dealing with sensory, cognitive, and behavioral aspects refer to honeybees (*Apis*) and bumblebees (*Bombus*), which have become the model organisms in insect neuroethological and behavioral investigations. This taxonomic bias, which may be justified by the easy rearing and maintenance of these social bees, is quite relevant in the context of (possible) plant-pollinator coevolution and reciprocal influences on diversification. Social bees from temperate latitudes are just a minute, almost biologically insignificant fraction of the broad set of animals that interact with angiosperms for pollination. Among insects, solitary bees, beetles, flies, moths, and butterflies are speciose and widespread pollinators, and there is no reason apart from convenience not to take them into consideration in cognitive ecology studies. Furthermore, our heavily biased knowledge of sensory and behavioral aspects of pollinators is in itself a hindrance to progress in our understanding of the role of pollinators in floral evolution, as is nicely illustrated in Weiss' chapter on vision and learning in some of these neglected pollinators. Assuming that what we know about the sensory and behavioral patterns of honeybees and bumblebees can be reasonably extrapolated to the full gamut of insect pollinators would be tantamount to accepting the principle that an insect pollinator is an insect pollinator, from the viewpoint of plants. This principle of "functional equivalence," apart from being contradicted by abundant biological evidence, would, if accepted, render logically untenable any explanation of diver-

sification of animal-pollinated angiosperms in terms of divergent selection from different pollinators. This leaves us with the conclusion that a body of knowledge based predominantly or exclusively on the behavior of a tiny group of temperate-habitat social bees will be intrinsically uninformative about the higher-level, grand question of whether there has been some evolutionary connection between the diversification of animal pollinators and animal-pollinated plants, just because it misses most of the very diversity that supposedly gave rise to angiosperms' diversification.

An outstanding exception to the prevailing pattern of evolutionary naïveté (or neglect) prevailing among animal-oriented chapters is Chittka et al.'s chapter on pollinator color vision and flower color evolution, which stands out among the strongest in the book. The chapter largely relies on, and summarizes, recent work by Chittka and associates on the evolutionary ecology of insect vision and its relationship to flower color. These investigations have provided important breakthroughs in our understanding of the evolutionary interrelationships between plants and pollinators (e.g., Chittka 1997; Chittka and Waser 1997; Briscoe and Chittka 2001; Chittka and Briscoe 2001). As many of these publications have appeared in non-American journals, this chapter provides a useful entry to this recent literature. Chittka et al. assess the extent to which evolutionary changes in flower color have been induced by selection pressures related to pollination, and whether the color vision systems of pollinators predominantly reflect adaptive evolutionary tuning to flower color. Contrary to expectations derived from coevolutionary views, there seems to be little empirical evidence of evolutionary matching of signals and receivers. As a noteworthy example, the distinctive elements of bee color vision were already present in arthropods originating more than 500 million years ago, well before the advent of angiosperms. Bee color vision is thus an exaptation with respect to flower color. Chittka et al. provide convincing examples suggesting that behavioral, sensory, and floral traits can be better explained by the species' phylogenetic history or constraints than by the assumption that each trait in each species is individually and optimally tailored to its environment. Furthermore, pleiotropy and indirect selection seem also to have played a significant role in the evolution of flower color, as when defensive products like anthocyanins have been later co-opted for pollinator attraction (Armbruster 2002). Chittka et al.'s challenging message is that genetic drift, pleiotropy, phylogenetic constraints, and chance have been sometimes more decisive than selection from pollinators in the evolution of flower color.

The spirit of Chittka et al.'s closing sentence, that "if we take alternatives to adaptation seriously, we may ultimately understand adaptation better," p. 123 also implicitly pervades Waser's final chapter on the "ethological isolation paradigm" (pollinator-mediated reproductive isolation as the major source driving speciation of animal-pollinated plants). By focusing on some of the paradigm's key assumptions, critically reviewing recent literature, and revisiting some classical examples supporting the paradigm (notably the familiar examples from the phlox family), Waser raises more than reasonable doubts about its prevalence in nature, let alone its universality, and suggests that intrinsic reproductive

barriers may evolve partly independently of floral phenotypic traits by which angiosperm taxa are usually recognized. In this scenario, Waser argues, the role of pollinators in plant speciation has probably been much more passive than in the strict ethological isolation paradigm, probably limited to indirectly facilitating microevolutionary differentiation and incipient reproductive isolation.

But stimulating and thought-provoking unorthodoxies do not stop here. In her chapter on pollinator-mediated assortative mating, Jones argues that for assortative mating to occur, divergent plant groups do not necessarily have to adapt to different pollinator taxa, and no selection directly on floral traits is required, as was implicit in the classical notion of pollination syndromes. Instead, the species or incipient species need to accomplish the relatively easy task of diverging sufficiently for individual pollinators to use *intraspecifically* variable traits (e.g., petal size) as a basis for constancy or labile preference, thereby improving pollen targeting. Jones presents several scenarios for pollinator-mediated divergence in sympatry and reinforcement of differences evolved in allopatry, as possible (and testable) mechanisms of diversification and maintenance of species boundaries in angiosperms. I found some interesting logical connections between some of her ideas and Waser's contention, noted earlier, that the role of pollinators in speciation may eventually boil down to an indirect facilitation of microevolutionary change. In addition, Jones' innovative extension of the notion of assortative mating to the intraspecific, sympatric context is also linked to, and supported by, evidence in Thomson and Chittka's chapter on individual (intraspecific) variation in pollinator behavior. Adopting a self-declared "evangelistic" stance, these authors outline some of the insights that are made possible by treating pollinators as individuals, and the possible pitfalls of not doing so. Considering individual variation in pollinator behavior is a first step suggested by Jones to test for possible instances of intraspecific assortative mating. There are still, however, at least two pending issues before the idea of intraspecific assortative mating as the "starter motor" of pollinator-mediated microevolution can develop into a full-fledged, coherent theory. First, we need to know whether individual variation in pollinator behavior of the sort documented in Thomson and Chittka's chapter, when it occurs, is consistent enough to provide the selection necessary to increase the frequency of variant floral phenotypes. And second, we need not only to consider and understand the bases of (intraspecific) individual pollinator variation, but also to consider whether there is consistent (intraspecific) variation among conspecific individual plants in the individual composition of their pollinators. Consideration of "pollinator individuality" advocated by Thomson and Chittka should be complemented by consideration of whether concomitant "plant individuality" exists too, and whether plant and pollinator individualities are consistently linked. Should this frequently happen, then intraspecific assortative mating, pollinator-mediated microevolution, and sympatric

divergence might possibly ensue in the way envisioned by Jones.

Despite its internal heterogeneity and weaknesses noted earlier, this book is a brave attempt at putting together new facts, ideas, and perspectives that are normally scattered in diverse sources. Borrowing Lewontin's (2000, p. 109) words, "It is easy to be a critic. All one needs to do is to think very hard about any complex aspect of the world and it quickly becomes apparent why this or that approach to its study is defective in some way." Plant-pollinator evolutionary interactions doubtless qualify, by and large, as one of the most complex systems ever faced by organismic evolutionary biology, so it is easy to identify things that could be done better. Although I would not recommend buying this book for one's personal library (at \$95), I do encourage pollination biologists to persuade their librarians to acquire it. To the more traditional plant biologists, several of the ideas and interpretations of Waser, Jones, Chittka, and others in this book (e.g., Smithson's skepticism on the actual importance of pollinator-mediated frequency-dependent selection *under field conditions*) related to angiosperm evolution and diversification may sound sufficiently heretical and controversial to spark lively discussions. For the young and/or more modern-minded, there are plenty of fresh, testable ideas to dig up. So, after all, Darwin's loose end about orchids continues to spur biological thinking more than one century afterwards.

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