

Preface

Radiations, or Evolution in Action

We have just celebrated the “Darwin Year” with the double anniversary of his 200th birthday and 150th year of his masterpiece, “*On the Origin of Species by means of Natural Selection*”. In this work, Darwin established the factual evidence of biological evolution, that species change over time, and that new organisms arise by the splitting of ancestral forms into two or more descendant species. However, above all, Darwin provided the mechanisms by arguing convincingly that it is by natural selection – as well as by sexual selection (as he later added) – that organisms adapt to their environment. The many discoveries since then have essentially confirmed and strengthened Darwin’s central theses, with latest evidence, for example, from molecular genetics, revealing the evolutionary relationships of all life forms through one shared history of descent from a common ancestor. We have also come a long way to progressively understand more on how new species actually originate, i.e. on speciation which remained Darwin’s “*mystery of mysteries*”, as noted in one of his earliest transmutation notebooks. Since speciation is the underlying mechanism for radiations, it is the ultimate causation for the biological diversity of life that surrounds us.

As we have learned, at the latest during last year’s celebration of Charles Darwin and his discovery of evolution, it was not only the immediate natural objects from the “*Beagle’s*” circumnavigation of the globe 1831–1836 that Darwin observed, collected and reported on that provided him with basal evidence for organic evolution. Even more important was his second, longer journey to discovery after his return to England, when Darwin developed his “*theory to work with*”, as he once wrote, after thinking about the Malthusian paradigm of the enormous fertility of organisms that surpassed the capacity of available resources. It was only through this second voyage during more than two decades, from early 1837 to his epochal publication in 1859 when Darwin patiently and dedicatedly substantiated his theory, that he truly completed the “Copernican Revolution” in biology. That way he finally brought “the origin and adaptations of organisms in their profusion and wondrous variation into the realm of science”, as Ayala and Avise recently pointed out (Proc Natl Acad Sci USA, 106 (2009): 2475–2476).

Around the globe, we have in 2009 commemorated two centuries of Darwin with numerous colloquia, conferences, cloud-gathering festivals, and museum exhibitions, and with new books and research articles in journals. The research papers compiled in the present volume also reveal some of the many aspects among the wide spectrum of current approaches in evolutionary research, following largely in Darwin's footsteps. In many ways, we today still relate to the plethora of observations and notes Darwin made more than a century ago. On the other hand, we have the privilege to use modern techniques, for example, from molecular biology and from systematic phylogeny, to allow the reconstructing of the relationships of organisms and the course of evolution – an accumulation of knowledge Darwin could not have imagined but that he certainly would have loved to know about.

Beyond doubt, Charles Darwin's contribution to our understanding of the origin of biodiversity cannot be overestimated, as a very natural transition will lead from the Darwin Year to 2010 as the Year of Biodiversity and Conservation. This book is a contribution to both celebrations, with the studies and model cases presented showing the progress and dynamic of research based on Darwinian theories as well as shedding light on the implications in context with the current biodiversity crises. The great importance of adaptive (and non-adaptive) radiations for biodiversity is widely accepted, but our understanding of the processes and mechanisms involved is still limited, and generalizations need to be based on the accumulation of more evidence from additional case studies. Our model cases are, more often than not, in need of being conserved, with their immediate habitats where we find and study them being better protected.

The studies presented in this volume are those urgently needed case studies focusing on a variety of organisms and different aspects of radiations. As case studies in evolution, they are also taking advantage of the progress in molecular biology and bioinformatics, two areas that have revolutionized modern biology. The scientific results presented herein are excellent examples not only of evolution in action, but also of active research on evolutionary processes and their most apparent outcome, viz. the biodiversity that we want to conserve for future generations to enjoy.

This volume aims at bringing together the immediate results of studies and projects conducted within a priority programme funded by the Deutsche Forschungsgemeinschaft (DFG) from 2002 to 2008 (see more on this in the following introductory chapter by Bill Martin). Here, the insights of 25 research groups with a total of 109 contributors are arranged in three parts: The first part (1) is concerned with approaches in botany (8 papers), the second part (2) with host-plant interactions (4 papers), and the third part (3) with approaches in zoology (13 papers); all summarizing the advances we have made so far.

The authors were asked to present their research with scientific rigor, albeit not necessarily presenting it in the usual form of a research paper, but if possible as a more readable review. That way, we have hoped to not so much write only for the few other experts in our immediate field of expertise (be it *Solanum* genetics, *Crematogaster* ants on Malaysian *Macaranga* plants, or *Tylomelania* snails in lakes on Sulawesi), but for a wider audience. At the same time, we hope to present

here a colorfully illustrated survey of current evolutionary biology research in Germany. These papers or chapters, although they were all independently written, are here grouped according to their main subjects, their hypotheses tested, and their major findings and implications. Of course, other arrangements are also possible; however, the present compilation follows an inherent design suggested by their contents that I will briefly outline here.

Starting with model cases for radiations in ferns on Madagascar (Schneider et al.), in plants on Macaronesian islands (Thiv et al.) and *Hordeum* in the Americas (Blattner et al.), a main underlying theme in this book will be the question of the driving forces responsible for species evolution. This is discussed, for example, for key innovations for ferns (Schneider et al.), the mating system in *Capsella* (Paetsch et al.) and, in particular, for ecological factors – the latter actually being the major recurrent factor in focus in many of the papers compiled here – such as pollinator-driven speciation in orchids (Ayasse et al.). The botany section concludes with two papers looking into population genetics and genetic diversity in plants used for human food, such as tomatoes (Stephan et al.) and wheat and barley (Kilian et al.).

In part II, four papers look at case studies in host–plant interactions as a special case of biotic evolution, searching for general principles that apply to those animals that directly live on, in or with plants and vice versa. The paper by Weising et al. discusses *Macaranga* speciation, the paper by Feldhaar et al. on speciation in *Crematogaster* adds the ant perspective to the story. Another intriguing case study on plants comes from the plethora of forms in wild roses interacting with fungi and insects (Kohnen et al.), while Johanneson et al. follow the traces of speciation in plant-dwelling tephritid flies.

Part III on the zoological approaches starts with examining radiations again and some of the proposed key factors responsible for diversification and speciation, exemplified by the incorporation of photosynthetic units in seaslugs (Wägele et al.), by the role of cuticular properties in fungus-growing termites (Marten et al.), and by the differential properties of the electric organ in African fishes promoting ecological speciation (Tiedemann et al.). With that, one of the major subjects of modern speciation studies is once more emerging, viz. testing the contribution of ecological versus geographical factors, as then also investigated in the paper by Schubart et al. on the adaptive nature of a radiation of freshwater crabs on Jamaica. The three subsequent papers look more specifically into the spatial component of speciation, using as exemplars the formerly assumed “ring species” of the *Larus* gull complex (Liebers-Helbig et al.), water frogs in the eastern Mediterranean (Plötner et al.), and hitherto cryptic species in Corsican *Limax* slugs (Nitz et al.). In addition to the latter paper that also deals predominantly with reproductive characters and properties, two more chapters examine the role of sexual selection in speciation, as illustrated for Cretan land snails by Sauer and Hausdorf, and by Mayer et al. for acoustically communicating grasshoppers, both in their way testing or providing evidence for non-ecological radiations. The possibility of sympatric speciation is further examined by Herder and Schliewen for lacustrine fishes in lakes on the Indonesian islands of Sulawesi. I am convinced that these central highland lakes provide us with a highly suitable “natural laboratory” for speciation studies, potentially even

better suited than other ancient lake systems, in order to test the differential role of allopatry versus sympatry, with a suite of geographical and ecological factors discernable, as shown for example in our own study of the endemic *Tylomelania* gastropods (Rintelen et al.). In the subsequent paper by Köhler et al., we further examine these themes for another closely related limnic snail group; however, this time not for a lacustrine but instead a riverine setting. Finally, the zoological section is complemented by another study on limnic snails (a group of invertebrates obviously on its way of being recognized as an emerging model system in evolutionary biology), with Wilke et al. investigating, this time explicitly, the possibility of non-adaptive radiations.

As is evident from the present compilation in this book, we are still far away from being able to provide a balanced view on radiation and speciation, as we are not even close to looking comprehensively at the major organisms, regions, or factors involved. While some taxa are examined herein very thoroughly, others are completely missing. Nevertheless, we discuss some of the most prominent factors and highlight future avenues of research. In any case, I am convinced that these papers presented here all show, in a variety of ways, evolution in action.

As authors of these papers as well as participants of the DFG priority programme, we are in great debt to the organisers, Klaus Bachmann and William Martin, who provided a major trigger for synthesizing our work. We are grateful for the financial support by the DFG and the continuous support by its representative, Roswitha Schönwitz, as well as grateful to the members of the review board for the many stimulating suggestions and discussions during these six exciting and successful research years, and to the reviewers of the 25 papers published here for their comments and constructive criticisms.

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