Matthias Glaubrecht
Editor

Evolution in Action

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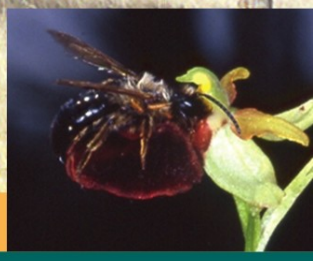

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In cooperation with Harald Schneider

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Case studies in Adaptive Radiation, Speciation and the Origin of Biodiversity

Special volume originating from contributions to the Priority Programme SPP 1127 "*Radiations: Origins of Biological Diversity*" of the Deutsche Forschungsgemeinschaft

Springer

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Cover illustration:

Top: Typical mound of termites species (*Macrotermes michaelseni*) at Kajiado, Kenya (from Marten et al., this volume; photography: Manfred Kaib).

Left: Wild tomatoes (*Solanum* sect. *Lycopersicon*): *S. chilense* from the Moquegua population, Peru (from Stephan & Städler, this volume; photography: Gabriel Clostre).

Middle: New and so far undescribed freshwater gastropod species of *Tylomelania* from Lake Poso on Sulawesi, Indonesia (from Rintelen et al., this volume; photography: Chris Lukhaup).

Right: Orchid *Ophrys sphegodes* with pseudocopulating males of the pollinator *Andrena nigroaenea* (from Ayasse et al., this volume; photography: Manfred Ayasse).

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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.

I would like to thank Harald Schneider who has helped during the review process with handling the botanical and host–plant interaction papers, Bill Martin for establishing contact with Springer, Heidelberg, and Sabine Schwarz and Anette Lindqvist of its Life Sciences Editorial Office for their encouragement and help throughout the process of editing this volume.

Berlin Matthias Glaubrecht
February 2010

Introduction to the Priority Programme "*Radiations: Origins of Biological Diversity*"

This book results from a focused research programme, a priority programme, that was funded by the German Research Foundation (DFG) during the period 2002–2007 entitled "*Radiations: Origins of Biological Diversity*" (priority programme SPP 1127). The programme was a landmark boost for studies in ecology and evolution at the species level in Central Europe, and it brought together a broad spectrum of evolutionary biologists, united by a single pressing question about the driving forces behind species diversification.

This is a good opportunity to answer a question that I have often been asked: how did the programme SPP 1127 come to be? Adjunct to the annual meeting of the German Botanical Society for 2000 in Jena, officers and representatives of the DFG invited a group of about 20 scientists from botany, zoology, microbiology, and ecology to a one-day brainstorming session on evolution and systematics, with the goal of identifying some of the big outstanding questions in the field, efforts towards whose solution would generate substantial progress in our understanding of biodiversity. It also had to be something harboring interest and research potential for those in the plant, animal, and microbial fields. Our brains astorm, and with the flames of discussion raging, we searched our gray matter hour upon hour for issues genuinely original, scientifically of outstanding value, and at the same time of broad enough appeal to attract the interests of chemists and physicists, for example, so as to be of obvious significance beyond a specialist audience. Good ideas are cheap. We needed a *great* idea. By mid-afternoon, things started to look pretty bleak, as did many faces around the table, and we had got to the point where we were discussing with mostly genuine enthusiasm things like "The postglacial recolonization of Europe", which is no doubt of great interest, especially for those of us living in Central Europe, but maybe not the biggest evolutionary topic ever identified.

Just when it seemed that there were no big questions left or otherwise identifiable in our storm-swept minds about species-level evolution, the waters parted. One of the world's leading botanists, Friedrich Ehrendorfer, opened up the afternoon session with the memorably booming words "Radiations! If we want to understand

the origin of species, we need to look where evolution is striding at its greatest pace." We all immediately recognized that a great idea had just been born, and from there on, the brainstorming was all downhill towards the goal of formulating a research proposal to the DFG with the aim of looking into the evolutionary impact of radiations, or evolution in action, as we have called it here in this book. That procedure entailed inviting several dozen potentially interested scientists to a colloquium in order to have short presentations and discuss the issue of radiations further, which we did; we being Konrad Bachmann, director of the Institut of Plant Genetics and Crop Plant Research in Gatersleben, Germany, and myself. That meeting brought the already considerable level of momentum to a point where people were suddenly expecting Konrad and I to write a proposal, as if we had signed some contract stating that we didn't have enough work on our hands and were desperately looking for more. It was at that time that I kept hearing things like "you write really well" from everyone in that circle, which I now understand to be a special kind of democracy known in most countries under the name of "mobbing". Only now do I notice that neither before that time nor thereafter had anyone ever directly commented on my writing skills.

Because the topic of radiations is rather broad, the priority programme (SPP) proposal that Konrad and I cobbled together contained some subtopics to help keep research efforts focussed. These subtopics were (1) the role of the reproductive system in speciation, (2) spatial separation and allopatric speciation, (3) the role of key characters in adaptive radiations, and (4) coupled radiations, where two or more groups seem to be cospeciating. It turns out that the SPP proposal was very popular with the decision-making bodies of the DFG, who earmarked rather generous sums for the study of species-level biodiversity on the basis of our document. Subsequently, the SPP proposal was also popular with the field in general, as an avalanche of outstanding individual research proposals came in for the first round. Over the six years that the priority programe SPP 1127 ran, the DFG allocated over eight million euros to fund 102 two-year research proposals aimed at species-level biodiversity. That substantial investment in basic science will return long-term benefits in our understanding of biological diversity and the role of radiative speciation processes in its origins. This volume summarizes some of the advances that emerged from projects that were funded during the priority programme. I hope that readers find it informative and attractive.

Over the course of SPP 1127, we held three successful colloquia, organized by Konrad and myself, and a very successful workshop on population genetic methods, kindly organized and run by Wolfgang Stephan and Thomas Städler from the Institute of Evolutionary Biology at the Ludwig Maximillian University in Munich. Various national and international activities in the field of biodiversity research emerged around SPP 1127 (a very notable one being the New Zealand Plant Species Radiations Network organized by Pete Lockhart of Massey University, with which several levels of interaction and exchange materialized), for which we are grateful.

Everyone associated with SPP 1127 owes special thanks to the programme's steering committee, who gave us good advice and assistance along the way. The steering committee was, in alphabetical order, Alfried Vogel (Natural History

Museum, London), Ian Baldwin (Max Planck Institute for Chemical Ecology, Jena), Spencer Barrett (University of Toronto), David Penny (Massey University, New Zealand), Edmund Gittenberger (National Museum of Natural History, Leiden, The Netherlands), Scott Hodges (University of California at Santa Barbara), Johannes Vogel (Natural History Museum, London), Dick Olmstead (University of Washington), and Wolfgang Wägele (Zoological Museum König, Bonn). Their time and their efforts in helping us to make the most of our research opportunities are very deeply appreciated. Thanks also go to Harald Schneider and Matthias Glaubrecht, who took it upon themselves to edit this volume.

All the participants in SPP 1127 owe the German Research Foundation and in particular Roswitha Schönwitz, our responsible programme officer who kept us on track from start to finish, an enormous round of special thanks for helping to make the program materialize. We also owe an equally special round of thanks to Friedrich Ehrendorfer from the University of Vienna for maintaining clarity of mind while the rest of our brains were storming away, and for coming up with the topic of radiations.

Düsseldorf
June 2009

William Martin

Contents