Symposium
&
9th Altenberg Workshop in Theoretical Biology 2002

VIENNESE ROOTS OF THEORETICAL BIOLOGY: THE VIVARIUM CENTENARY

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organized by Manfred Laubichler, Gerd B. Müller, and Werner Callebaut

Konrad Lorenz Institute
for Evolution and Cognition Research
Altenberg, Austria
&
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The topic

Theoretical biology emerged as a discourse among biologists from a variety of different experimental disciplines and some philosophers and physicians during the early decades of the 20th century. This discourse was centered around the conceptual, epistemological, and methodological foundations of biology as well as the relation of biology to physics and metaphysics (the problem of the autonomy of biology), mathematical modeling of biological processes (such as regulation, differentiation, inheritance, and organic transformation), and the representation of biological knowledge. It engaged many of the foremost biologists of Europe (Germany, The Netherlands, Austria, Russia, and Britain) and, to a lesser extent, the United States.

Vienna has traditionally been a fertile ground for discussions related to theoretical biology. Several prominent members of the Vienna Medical School, arguably one of the leading centers of Medicine at the turn of the 20th century, had a strong interest in conceptual problems of biology and medicine; research in experimental and theoretical physics explored problems related to biology; Ernst Mach's approach to history and philosophy of science was based on an evolutionary (or adaptationist) approach to knowledge. Last but not least, the Vivarium, an initially private Institute for Experimental Biology fostered research into the theoretically relevant problems relating physiology,development and environmental modification.

On the year of the 100th anniversary of the foundation of the Vivarium the workshop will explore the historical roots as well as the legacy of theoretical biology in Vienna. It will focus on the history of the Vivarium and investigate the careers and contributions of important figures associated with it (Przibram, Kammerer, Exner, Weiss, von Bertalanffy). But the workshop is also intended to raise larger themes and open up fresh perspectives for theoretical biology in the 21st century. There will be papers that place the Viennese tradition in the larger context of modeling biological processes, explore the history and future perspective of research into the role of the environment in development, and analyze the significance of extra-university settings and research institutes in both the past and present. Finally, today´s role of theoretical biology in integrating the life sciences will be analyzed.

Program

SYMPOSIUM at the Austrian Academy of Sciences, Vienna

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Abstracts

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Paul Weiss: A Life Between "Resonance" and Controversy

In 1931 Paul Weiss, who was born in Vienna and trained at the Vivarium, entered the United States to collaborate with Ross G. Harrison on tissue culture. Two decades later he had established himself as a brilliant experimental biologist who had discovered the axonal transport of peripheral nerves and invented a new surgical technique to bridge cut nerves without sutures. In developmental biology he explained the mechanisms of cell contact and investigated the self-sorting of embryonic cells. However, what distinguished him from many biologists of his time was the emphasis he laid on a theoretical approach towards the organismic cell. To encompass the complexity of this living system, he formulated an intricate dictionary of concepts. Here I will sketch the life-long controversy between Paul Weiss and his graduate student Roger W. Sperry on the crucial issue how to explain the neuromuscular regeneration after transplantation. Roger Sperry opted for Cajal's chemo-affinity, and his mentor Paul Weiss for the resonance principle which he corroborated with the concepts of contact guidance and neural specificity. Despite the thorny problem to make feasible the experimental data to one's own working hypotheses, the dispute shows how deeply experimental scientists rely on a sound definition of their concepts.

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What Theoretical Biology Can Do — and What it Cannot: Model Systems and Model Building in Developmental Biology see Denis Thieffry

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Ludwig von Bertalanffy and the Difficulties With Any Theoretical Biology

Bertalanffy´s program for a Theoretical Biology and his General System Theory are reassessed from a contemporary philosophical perspective. Current philosophy of biology is more radically naturalistic and more critical with respect to the idea of a unity of science than his view. I evaluate his claims concerning the autonomy and irreducibility of biology in the light of post-positivist insights into the dynamics of science. I argue that the elaboration of a Theoretical Biology could benefit from a stricter separation between the explanatory interests of science and the idiosyncratic demands of an author´s Weltanschauung or metaphysics.

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The Przibram Brothers and the Border Regions of Biology

Historians have generally overlooked key collaborations between biologists and physical scientists in early twentieth-century Vienna, some of which produced projects that foreshadowed later trends. Some of the most fruitful cross-fertilizations came from two pairs of brothers, Sigmund and Franz Serafin Exner and Hans and Karl Przibram, scientists from two of Vienna’s renowned dynasties of scholars. Both families cultivated what nineteenth-century pedagogues termed many-sidedness, a typical Austrian bourgeois value that made interdisciplinarity attractive. Yet the families’ differences will prove as instructive as their similarities. I will consider two joint projects: the Exners’ investigations of color perception in different species, and the Przibrams’ plan for a general morphology of natural forms. Typical of Vienna’s cultural elite, both pairs found their motivations in aesthetic concerns. In fact, each vision of scientific unification rested on a universalized aesthetics. Yet while the older pair defended classicism, the younger embraced Secessionist modernism. Ultimately, these two long-lived projects are windows onto the changing significance of cross-disciplinary science for two Viennese families from one world war through the aftermath of the second.

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Interdisciplinary Research Outside and Within the University

Excellence in biology requires specialization to understand leading research questions, sophisticated equipment, and complex methods, but much of today's exciting research requires breadth to draw on several disciplines and subdisciplines. Resolving the specialization versus generalization tension preoccupies many biology departments. No organizational structure can satisfy all of the sometimes contradictory needs of specialization and generalization, but multidisciplinary and interdisciplinary programs give a diverse group of faculty members a common ground on which to meet. The best contemporary research and training demand intellectual agility, quick assessment, rapid response to information, plus an openness to embrace new ideas from diverse disciplines. These values often have multidisciplinary and interdisciplinary thinking as endpoints. Increasingly, research and training

programs encourage collaboration, placing a high value on collegiality and cooperation.
One way to appreciate the complexity of decisions at the intersection of subdisciplinary diversity, personalities, and forces internal and external to the university is to consider a specific case. I will review the recent history of the Biology Department at Arizona State University as an example of how multidisciplinary and interdisciplinary research and training programs can provide life science departments a way to foster the innovation needed to cope with rapid change in biology. Likewise, I will discuss how the National Science Foundation is using various strategies in biology and environmental sciences to provide funding opportunities for large scale research projects that are interdisciplinary, integrative, and can span levels of organization from molecular biology to ecosystems ecology.

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Signals From Above: Ecological Induction of Phenotypic Patterns

Epigenesis concerns the interactions through which the inherited potentials of the genome become the adult. In addition to epigenetic interactions occurring within the developing embryo, there are also critical epigenetic interactions occurring between the embryo and its environment. These interactions can determine the sex of the embryo, increase its fitness, or even be involved in the formation of particular organs. This essay will outline the history of environmental concerns in developmental biology, provide some reasons for the decline and resurgence of these ideas, and will then focus on two areas that have recently gained much attention: predator-induced polyphenisms and developmental symbioses. Research in these two areas of interspecies cooperation in morphogenesis has profound implications for what we consider to be normal development and how we proceed to study it. Studies of predator-induced polyphenism have shown that soluble factors from predators can change the development of prey in specific ways. Prey has evolved mechanisms to sense compounds released from their predators and to use these chemical cues to change their development in manners to prevent predation. New techniques in molecular biology, especially polymerase chain reaction and microarray analysis have shown that symbioses between embryos and bacteria are widespread and that animals may use bacterial cues to complete their development.

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The Spoiler: Paul Kammerer's Fight for the Inheritance of Acquired Characters

In scientific controversy, as in sports, there are usually winners and losers, but in Paul Kammerer's fight for the inheritance of acquired characteristics, the outcome was not so simple. To be sure, Kammerer's precise ideas about variation and heredity, i.e., that environmental effects on the organism could be recorded in the form of new genes on chromosomes, never had much support, and his suicide following the midwife-toad scandal silenced the few allies still with him in 1926 and sealed his reputation as a fraud. Yet Kammerer's work had caused repeated uproars in the scientific literature and elicited detailed — and contradictory — rebuttals by champions of Darwinism, neo-Darwinism, and Mendelism. Who, if anyone, had a theory superior to Kammerer's?

Was it William Bateson, with his saltational Mendelism (minus the chromosome theory)? Erwin Baur, with his paired concepts of "mutation" and "modification"? Ludwig Plate, with his dual system of Mendelian-chromosomal and somatic-cytoplasmic inheritance? August Weismann and his germplasm-determinants? Before 1927, these were the leading alternatives.

In this paper, I treat Kammerer as that special kind of loser, known to sports fans as the "spoiler": the unheralded outsider, whose unconventional tactics allow him to surprise and embarrass the established stars of his discipline and expose their weaknesses. I retell the story of Kammerer's life and work, showing how he used his outsider's position and unique laboratory results to provoke the experts, expose their disagreements, and sow confusion about the nature and origin of variation. I suggest that the Kammerer controversy was not primarily about Kammerer's results or his specific theory, or the inheritance of acquired characteristics more generally, but about how else heritable variation might be produced. In 1926 it was easier to label Kammerer a fraud than to answer that question.

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Non-University Research Institutions in Vienna and Naples

In Naples, in 1872 the German zoologist Anton Dohrn founded the first independent research facility at the seashore. An unusual mixture of personal experience, vision, encounters and conviction, mixed with a good dose of luck and ingenuity had led to this moment in history. Due to Dohrn's initiative skill this started a new epoch in research. Freedom for research, well equipped laboratories, most recent methods, peer contacts, an excellent library, and a perfect supply of research material were among the factors that made the Naples Station an unrivalled international research center. Dohrn's administration and management were also innovative: he optimized resources and rented out work space. The so-called "table system" guaranteed a stable income on a commercial basis. Austria rented 2 tables from 1874 to 1876 and again from 1888 for 30 years. They were used over 140 times by Austrian scientists, mostly from Vienna. The Naples Station will serve as a good example to highlight the role of Marine Stations in general and their significance for experimental biology in particular.

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The Role of Theoretical Biology in Integrating the Life Sciences

During the last century the life sciences have grown so quickly that we speak, for example, of the 'molecular revolution'. A high degree of diversification went along with this growth and lead to ‘centrifugal forces’ that seem to divide biology into a number of different disciplines. Each of these disciplines develops models and concepts from a highly specialized perspective and in doing so develops its ‘private’ domain of theory. This is a consequence of the otherwise extremely fruitful reductionist attitude of researchers in the life sciences. Undoubtedly, reductionism is the powerful principle that led to the molecular revolution. However, the study of detail becomes particularly meaningful if ‘bits and pieces’ can be put together in a ‘grand picture’. Theoretical biology aims at giving this picture. In order to achieve this goal, it is helpful to compare how the organism’s regulatory systems, such as that of the cell cycle or of the immune response, solve similar problems. For example, all these systems have to cope with the problem of reliability of their molecular switches and signal transduction pathways in the presence of noise, cross talk, and faulty components. In using the comparative analytical approach, theoretical biology can identify how the structural design of regulatory systems reflects these robustness problems. The comparative approach enables us to reveal general design principles of living systems but it also helps us to better understand the special properties of different regulatory processes.

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Consensus and Conflict in Viennese Biology: A Short History of the Prater Vivarium

My paper provides an overview of the foundation of the Prater Vivarium, the different phases of its development, and the hitherto untold history of its dissolution in the Nazi period. The driving force behind the the foundation of the Vivarium in 1902 was Hans Przibram. It is interesting to see how he selected his collaborators and his local and international partners in order to achieve a well-defined scientific profile. Yet throughout the years and despite its growing international recognition the Vivarium enjoyed mixed relations with the other local institutions active in biological research and academic instruction, in particular, the University of Vienna, the Museum of Natural History, and various learned societies, among them the influential Zoologisch-Botanische Gesellschaft. I develop the Viennese controversies on the method of biological research by highlighting basic concepts such as evolution and heredity, and by reconstructing their differences on whether biological research should focus on certain model animals,, or cover the maximally possible variety of species. I further discuss how these issues were embedded into diverging political world views and how they found their expression in a complex network of personal encounters. After the Anschluß, the founders of the Vivarium quickly fell victim of racial persecution. The various attempts to take over the experimental laboratory led into a confrontation exhibiting a telling interplay of academic and political arguments.

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The Viennese Roots of Theoretical Biology

Theoretical Biology emerged as an interdisciplinary discourse rather than an established discipline at the turn of the 20th century. Vienna has traditionally been an especially fertile ground for the development of Theoretical Biology. While the Prater Vivarium and the Medical Faculty at the University of Vienna have been the institutional centers of Theoretical Biology in Vienna during the first decades of the 20th century, many of the actual ideas were nurtured in more informal settings. Some of these specifically Viennese elements of the international discourse of Theoretical Biology will be presented as part of the symposium papers that analyze the contributions of individual scientists associated with the Prater Vivarium. This introductory paper will briefly sketch the history of Theoretical Biology in Vienna, the main intellectual agendas associated with it, as well as the institutional development of the field. I will also introduce a largely unknown early participant in these debates, the pediatrician Max Kassowitz. The paper will conclude with some reflections on the nature of Theoretical Biology and its possible future role within the rapidly changing landscape of the Life Sciences, both in Vienna and abroad.

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Experimental Strategies of Vivarium Research

The Biologische Versuchsanstalt "Vivarium" was devoted to the study of the relationship between environment, development, and evolution. The institute was designed and equipped to promote experimentation involving whole organisms, and their entire life cycles, over several generations and under variable environmental conditions. I will discuss the implementation of the experimental program, some of its major topics and results, and the changing design of experiments in accordance with shifts in programmatic emphasis. It will be pointed out that the Vivarium was an institution not only of experimentation but also of quantification and thus helped pave the way for mathematical abstraction and the conceptualization of organismal theoretical biology. I will close on a few notes about the legacy of the Vivarium movement for what today is called Evolutionary Developmental Biology.

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Vivarium Concept and Eco-Evo-Devo Aspects in Regeneration Studies

Studies of regeneration lie at the origin of "experimental" zoology as well as of developmental biology. In the early decades of the last century regeneration research was one of the major subjects, not just in embryology (now Developmental Biology), but in zoology at large, and was one of the core issues at the Vienna Vivarium during this period. My talk concerns the historical significance of these studies,

emphasizing their pioneering role in modern developmental biology. In particular, I would like to mention the work of Professor Hans Przibram, a founder of the Vivarium. His far-sighted interest in “heteromorphosis” in the regeneration of appendages should be emphasized.
Regeneration is generally a replication of preformed structures, but in rare cases it involves heteromorphic regeneration. Heteromorphosis occurs in, for example, the regeneration of antenna-like organs after eye removal. At the Vivarium a number of reports on heteromorphosis based on experiments and observations of individual insect specimens collected from nature were published by Przibram and his colleagues in the 1920s and 1930s. Subsequently, geneticists also discovered heteromorphic mutants in Drosophila. Studies of heteromorphic mutants in the 1970s resulted in the discovery of the homeobox. This marked a reformation of developmental biology in general and has opened links between developmental studies and evolutionary biology (Evo-Devo).
At present we know heteromorphic regeneration in Vertebrates as well. The occurrence of heteromorphosis will renew our interest in the question of the evolutionary significance of regeneration in nature. This necessitates the reassessment of the significance of the capability of regeneration for maintaining the viability of organisms (Eco-Evo-Devo).
Regeneration studies went through a dark period in the middle of the 20th century, but they are now being revived. No doubt there are opportunities, particularly in heteromorphic regeneration, to find vast hidden potentialities of living organisms from the philosophy of “organicism.” Research at the Vivarium looked for the background not only through philosophy, but through experiment and observation.

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Experimental Systems and Theoretical Reflection

In this paper, I would like to present an overview of the theory constraints and the theoretical possibilities that come with the deliberate organization of biological work in experimental systems. With experimental systems, theory and practice in biology enter in a new relationship. I would like to point at a few consequences that this situation — in particular the delineation and interconnection of experimental systems — may have for the elaboration of concepts and theories in biology.

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From Mendel to Theoretical Biology in the 20th Century

Gregor Mendel was the first biologist who used a model based on mathematics for the interpretation of his experimental results and statistics for the evaluation of data. By choosing an appropriate system he could reduce the enormous complexity of inheritance to observation depending (almost) exclusively on

single genes. Thereby he revealed and discovered the mechanism of genetics which found its explanation by molecular biology only in the second half of twentieth century. Wholistic description of nature is what we seem to be heading for, but reduction, although unpopular with a high percentage of macroscopic biologists, provides the fuel that drives the engine in the progress of understanding. In my note I will present a broad and comprehensive view of theoretical biology that also includes theory, structure, and function of biomolecules, and confront it with narrower conventional concepts, in particular, population genetics, theoretical ecology, and epidemiology as well as systems biology. Accordingly, names of scientists from Vienna and Austria, not discussed by other speakers, will pop up in my contribution, for example Max Perutz, Erwin Chargaff, Wolfgang Braunitzer, and Emile Zuckerkandl, who pioneered structural biology and comparative sequence analysis of biopolymers. Similar to Mendel, they made important contributions to the basis of knowledge in biology by conceiving and carrying out appropriately chosen experiments based on theory driven insight. Finally, I shall review the current state of systems biology where we watch the beginning of successful integration of molecular knowledge into organismic thinking by network theory based on functional genomics.

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What Theoretical Biology Can Do — and What it Cannot: Model Systems and Model Building in Developmental Biology

In this presentation, I will start with a concrete example of model building in developmental biology, addressing the issue of how the formation of segmental borders is genetically controlled during early Drosophila melanogaster development. Leaning on this example, I will emphasize:
1) the different kinds of data available to the modeller;
2) the variety of assumptions to be made before reaching a consistent model;
3) qualitative versus quantitative issues;
4) the productive power of modelling analyses.
Going through this example should also provide some support to more general discussions on the role of 'model organisms' as well as on that of 'mathematical model analyses', both in the context of developmental and evolutionary studies.

Building on Denis Thieffry's presentation plus our knowledge of evolutionary tinkering and the ways development is controlled, I argue for some limitations on the generality of results obtainable by use of model organisms and by mathematical modeling in developmental biology. Granting the value, power, and necessity for working with both kinds of model, I explore whether we can usefully characterize limitations pertaining to available models. One class of limitations stems from features of developmental processes. For example, the recycling of various control and signal transduction systems into different ontogenetic and phylogenetic contexts shows that understanding specific connections among parts and processes is important for understanding development. This result places limits on "bottom up" analyses of development and on the generality of results obtained with model organisms.

Another sort of limitation, commonplace among mathematical modellers, applies to work with model organisms as well: every model embodies tradeoffs among such desiderata as “realism,” “precision,” and “generality” (labels taken from Richard Levins). Thus, both substantive considerations and the multiple, conflicting aims of modeling set limits on what theoretical biology can accomplish in the analysis of development.