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Introduction to the Papers of the 2001 Kowalevsky Medal Winner Symposium

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In 2001, the centennial of Alexander Kowalevsky's death, the St. Petersburg Society of Naturalists re-established the Kowalevsky Medal honoring ''extraordinary achievements in comparative zoology and embryology of the scientists who have contributed greatly to the modern understanding of evolutionary relations between major groups of the animal kingdom, the evolutionary biology of development, and modern approaches in comparative zoology.'' The Medal together with a small monetary reward was originally established in 1910, yet the political turmoil of the 1910s—World War I, the Russian Revolution followed by Civil War—interrupted the process of establishing and awarding the Medal and Prize. During Czarist Russia the St. Petersburg Society of Naturalists was a well respected Learned Society with many international ties and the nomination process for the Kowalevsky Medal was always intended to involve the whole international scientific community. But the Kowalevsky Medal was not a priority for the Society during the difficult times following the Civil War and the Prize and Medal faded into (temporary) oblivion. Not all was lost, however, as the original cast for the Medal was preserved in Leningrad's (St. Petersburg's) Hermitage Museum. It has recently been discovered and the St. Petersburg Society of Naturalists decided to reinstate the Prize and medal on the occasion of the Kowalevsky centennial (see Mikhailov and Gibert, 2002 for more information on Kowalevsky and the Medal).

At the December 2001 meeting of the St. Petersburg Society of Naturalists the first winners of the Kowalevsky Medal were announced. As was originally intended, the winners were selected based on recommendations of an international group of nominators. The winning group of eight biologists from seven different countries represents a wide spectrum of biological sub-disciplines as well as local traditions. The winners are: D. Anderson (Australia), G. Freeman (USA), B. Hall (Canada), O. Ivanova-Kazas (Russia), C. Nielsen (Denmark), R. Raff (USA), R. Riedl (Austria), and K. Sander (Germany). In subsequent years one Kowalevsky Medal will be awarded annually.

Following the announcement of the first cohort of Kowalevsky Prize winners the Division of Evolutionary Developmental Biology of the Society for Integrative and Comparative Biology sponsored a symposium at its January 2003 meeting in Toronto. At this meeting several of the Kowalvesky Medal winners responded to this honor. The papers collected in this issue of Molecular and Developmental Evolution are revised and expanded versions of the symposium presentations. Together these papers provide a unique opportunity to trace the multiple roots of the modern re-synthesis of evolutionary and developmental biology that during the 19th century was associated with names such as Ernst Haeckel, Francis Balfour, and Alexander Kowalvesky.

The reinstatement of the Kowalvesky Medal was timely. By all accounts ''evo-devo'' has arrived. It is now solidly entrenched in the conceptual framework of modern biology and has all the markings of a new discipline, such as representation in professional societies, scientific journals devoted to the field, academic programs and job searches, panels at funding agencies, textbooks, etc.. However, current-day evolutionary developmental biology is not as uniform as the image of a new scientific discipline and the powerful icons of ''the genetic toolkit for development'' and the almost magical qualities of ''Hox genes'' seem to suggest.

As a matter of fact there are many different questions currently pursued under the umbrella of

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evolutionary developmental biology, such as the developmental and genetic basis for evolutionary change, the evolution of developmental mechanisms, the origin of evolutionary novelties, the reasons for conserved patterns of morphology, the origin and diversification of animal and plant forms, etc. These fall under several organizing categories that are even reflected in the three most widely used acronyms for the field; ''evo-devo,'' ''devo-evo,'' and ''developmental evolution.'' It is certainly a sign of a healthy intellectual climate that we currently have a lively debate about these conceptual questions accompanying the empirical and theoretical work in the field and it is a credit to the editors of our journals and the officers of the DEDB division that they encourage these discussions in print and as part of symposia [e.g., the inaugural symposium of the DEDB division of SICB—see American Zoologist 40(5) 2000; Editorials and Perspectives Papers in *Evolution & Development* and *Molecular and Developmental Evolution*; or the special issue of *Biology and Philosophy* devoted to Evo devo—Biology and Philosophy 18(2) 2003].

Related to the conceptual discussions about the basic theoretical structure of evolutionary developmental biology are questions about future research directions. Insofar as these questions also involve decisions about the allocations of scarce resources building consensus while maintaining diversity will be crucial for the future of the field. This brief introduction to the Kowalvesky symposium papers is not the place to go into any more details about these issues, safe of the fact that history, represented here by several unique perspectives of scientists from different intellectual traditions, who began to pursue evo-devo questions before there was ''evo-devo,'' and certainly before there was any knowledge about the Homeobox, and whose work reflects diverse comparative, systematic, developmental, and theoretical perspectives, can serve as a valuable guide for current practitioners in the field.

Indeed, there is barely another field in biology that has self-consciously employed its history to the extant evolutionary developmental biologists routinely do (e.g., Gould, '77; Hall, '92, '99). There are many reasons for this trend (see Laubichler and Wagner, 2003), but it is obvious that the history of problems, approaches, and observations matters to present-day evolutionary developmental biologists. The field has also attracted the attention of historians and philosophers of biology and several workshops and volumes are currently in preparation of in press (e.g., the Dibner volume on the history of evolutionary developmental biology edited by Laubichler and Maienschein) as well as the series of vignettes in the history of evolutionary developmental biology in this journal (see Hall, 2003; Laubichler, 2003) for the first two vignettes).

The way we perceive the field today is often reflected in the way we reconstruct its history and, similarly, the way we present the history can reveal a lot about current assumptions. Several themes stand out in recent discussions about evolutionary developmental biology and its history. One theme is the emphasis that ''evo-devo'' represents a new synthesis or that it completes the Modern Synthesis, which had largely ignored development. Another, championed among others by Brian Hall, is the view that evolutionary developmental biology brings together many more disciplines and approaches than just developmental and evolutionary genetics (e.g., Hall, '99). In a similar vain, Love and Raff (2003) have argued for the inclusion of a tradition of comparative embryology, but have mostly focused on the British and American literature. And Scott Gilbert has argued that ecology needs to be incorporated more forcefully into evolutionary developmental biology, thus eco-evo-devo, and has presented several historical arguments to support his claim (e.g., Gilbert, 2001; Gilbert and Bolker, 2003).

In light of all these discussions the papers collected here add some important new perspectives. They give us first hand accounts of how some of the leading practitioners in the field perceive their own role, the development of their research in evo-devo (to a large extant before there even was such a field in the modern sense), and the emergence of the discipline. The papers also reveal a lot about the many different intellectual, educational (esp. Hall and Riedl), and scientific contexts that have shaped present day evo-devo. These papers thus support the claim that evolutionary developmental biology is an intellectual and scientific enterprise that has many roots, has emerged in many different intellectual traditions, has a rich and complex history that reaches back into the 19th century, and was quite lively even before the homeobox has first been discovered. Indeed, the main conferences that have defined modern-day evolutionary developmental biology, such as the Dahlem conference on ''Evolution and Development'' in 1981 in Berlin, Germany (Bonner, '82), the symposium of the British Society for Developmental Biolgy on ''Development and

Evolution'' in 1982 at the University of Sussex, and the ''Field Museum Conference on Macroevolution'' in 1983 in Chicago; all took place before the discovery of the universality of the homeobox in 1987 (Schughart et al., '87).

In light of these important pre-Hox events, Brian Hall, who is not only the author of one of the major textbooks in the field, but also one of the most knowledgeable historians of evolutionary developmental biology gives us a unique perspective on the ''education of an evo-devoist.'' His autobiographical account provides insights for both biologists as well as historians; biologists are reminded how important it is to give and receive a broad and wide ranging education in many different disciplines, if one plans to work in areas that require the ability to synthesize large amounts of data and methodologies and historians are reminded about the importance of local educational practices and the fact that discussions about the relationship between development and evolution need to be placed within a larger international context of the history of 19th and 20th century biology. The reading list for upper division zoology is particularly instructive and might inspire others to send us similar pieces of information as such items will be indispensable in reconstructing the intellectual lineage of evolutionary developmental biology.

Rudy Raff and Alan Love's paper contextualizes Rudy Raff's longstanding research program within both the conceptual as well as the technological advances of the last decades in the history of evo-devo and of biology at large. This paper also goes a long way to help us understand the inner workings of the development and diversification of evolutionary developmental biology. Their distinction between lineages of problems and lineages of tools is extremely useful. It allows us to recognize the many ways how technological advances or limitations can shape the fate of scientific disciplines and research programs. In the case of evolutionary developmental biology with its long tradition reaching back into the 19th century this distinction also emphasizes the conceptual continuities between the past and present.

In their paper Klaus Sander and Urs Schmidt-Ott follow William Bateson's approach in the ''Materials for the Study of Variation.'' They compile a series of facts and observations, both ''classical'' and ''molecular'' that illustrates the continuity of problems as well as the progress in understanding the molecular mechanisms of development within an evolutionary context. This paper is another account from a participant's perspective of how major technological and scientific developments fit together. It also brings to our attention the important and, at least in the modern historiography of 20th century biology, often overlooked role of local European traditions in the history of evolutionary developmental biology.

Günter Wagner and Manfred Laubichler's paper attempts to explain Rupert Riedl's contributions to evolutionary developmental biology''in the language of modern biology,'' as Riedl charged the authors to do. In addition, this paper also places Riedl's career within the context of morphology, marine invertebrate zoology, and theoretical biology as it developed in Vienna during the 20th century. As Riedl's work is among the more theoretical and conceptually oriented contributions to evolutionary developmental biology, the inclusion of Riedl among the Kowalevsky Medal winners also signifies the recognition of these efforts as a legitimate part of evo-devo. This, again, is not without historical precedent, and, as the career of Ernst Haeckel demonstrates, can be an extremely stimulating as well as controversial part of the discipline.

Claus Nielsen's recognition as a Kowalevsky Medal winner is a well-deserved reminder of how important systematic and comparative biology are for all the other disciplines. Morphology and comparative anatomy dominated 19th century zoology and provided the context for the emergence of both evolutionary as well as developmental biology, yet today many tend to reduce comparative biology to molecular systematics. While it is true that molecular techniques paired with cladistic analysis can address many important questions in phylogeny, they are by no means a substitute for the extremely difficult work of comparative zoology. Many problems of evolutionary developmental biology can only be addressed within a framework of comparative biology and, on a more prosaic level, we all expect to be able to find reliable information about all major sytematic groups. Claus Nielsen's discussion here and in his other works (e.g., Nielsen 2001) highlight the importance of these problems.

In short, the papers collected in this issue help us to understand the broader scientific, intellectual and cultural context for the emergence of 21st century evolutionary developmental biology.

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