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Interview

Putting evo-devo into focus

An interview with Scott F. Gilbert

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"Indeed, if you seek the intellectual challenges of building new concepts, developmental biology is the place to be." (Gilbert, 2003a)

Developmental biologists seek to understand how a sophisticated complex multi-cellular adult form can arise from a single fertilized egg. Evolutionary biologists look at adult forms to understand how they could historically evolve. Recently, developmental biology and evolution research have overlapped, generating a new field, evolutionary developmental biology (often referred to as "evo-devo").

In the year 2004, Scott F. Gilbert, Professor of Biology at Swarthmore College and one of the founders of evo-devo has been awarded the prestigious Kowalevsky Medal** for outstanding contributions to the field, before and after evo-devo had a name. Notice of this award was received in late November from the Council of The Saint Petersburg Society of Naturalists. Professor Scott Gilbert shares this honor with other leading researchers in the field, such as Professors Brian Hall, Rudolf Raff, Eric Davidson, Walter Gehring and Olga Ivanova-Kazas to name a few.

Dr. Gilbert's textbook, *Developmental Biology*, brought evolutionary insights into the introductory developmental biology course and helped make this area part of normative developmental biology. In 1997, he and his wife published *Embryology: Constructing the Organism*, the first comparative embryology book in English for over 100 years (Gilbert and Raunio, 1997). Dr. Gilbert has also written numerous influential articles in evolutionary developmental biology, including the manifesto-like "review" (co-authored with John Opitz and Rudy Raff) in 1996 that helped justify the existence of this new field (see Gilbert *et al.*, 1996). In 2001, he wrote another influential essay bringing together the diverse areas of ecological developmental biology into a coherent framework (Gilbert, 2001). In both cases, these essays were presaged by chapters in his book.

Dr. Gilbert has also brought together people from different areas of biology to discuss evolution and development and has brought the synthesis of evo-devo to many places. In 1990, he organized, with J. W. Atkinson, the first conference in America on evo-devo at

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*** Alexander Kowalevsky was a 19th-century Russian embryologist and a Darwinian whose studies of amphioxus and tunicate larvae united the invertebrate and vertebrate regions of the animal kingdom. In 1910, the St. Petersburg Society of Naturalists had established an international award in commemoration of Alexander Kowalevsky's legacy. The inauguration of this project was first interrupted by the First World War followed by the Russian Revolutions, Civil War and "Gulag" , and then by the Second Word War and more than 25 years of obscurantism in Soviet biology led by Trofim Lysenko together with his devoted comrade Isaac Prezent. Fortunately, a small group (Sofia M. Efremova and Nataliya I. Balakhonova) headed by Professor Archil K. Dondua at the University of St. Petersburg took measures that culminated in recovering the Kowalevsky award and its medal. Dr. Efremova found the original Kowalevsky Medal in "Hermitage" archives, whereas Balakhonova looked for the Medal molder at the Museum of "Coin's Court" (Saint-Petersburg, Russia). In 2000, the St. Petersburg Society of Naturalists was pleased to announce the re-establishment of the Alexander Kowalevsky International Prize (i.e., The Kowalevsly Medal) for outstanding contributions in the fields of evolutionary developmental biology and comparative zoology (for details and commentaries, see Dondua and Aleksandrov, 2002; Mikhailov and Gilbert, 2002; Raff et al., 2004).*

Note: Drs. S.F. Gilbert and A.T. Mikhailov dedicate this essay to the memory of their mutual friend, molecular developmental biologist, Dr. Alexander A. Karavanov who died at his home on Monday, 24 January, 2005.

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ДИПЛОМ
С.-Петербургское Общество Естествоиспытателей

присудило медаль
Александра Онуфриевича
Ковалевского

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За многолетние исследования и выдающиеся результаты в области сравнительной зоологии и эволюционной эмбриологии

решением Ученого Совета Общества
в Санкт-Петербурге

22 ноября 2004

DIPLOMA
The St.Petersburg Society of Naturalists

awards
Alexander Kowalevsky medal
to

Dr. Scott Gilbert

For life–long research and extraordinary achievements in the field of comparative zoology and evolutionary embryology

awarded by the decision of Society's Council
in St. Petersburg

November, 22, 2004

проф. А.К.Дондуа, президент

М.А.Савченко, секретарь

Fig. 1. The St. Petersburg Society of Naturalists awards the "Kowalevsky Medal" to Dr. Scott F. Gilbert. (A) *Recipient of the Medal, Scott Gilbert, sitting beneath a picture of K.E. von Baer in von Baer's house in Tartu (Estonia, 2003).* **(B)** *A copy of the award diploma.*

the annual meeting of the American Society of Zoologists. Ten years later, when that society (which had become the Society for Integrative and Comparative Biology) inaugurated the new division of evolutionary developmental biology, Dr. Gilbert organized the foundation symposium that helped establish the discipline and he served as acting chair of the new division. In 2002, Scott brought together people from many disciplines for the first symposium on ecological developmental biology.

Dr. Gilbert's has written on such topics as modularity, homology, canalization, complexity and the origin of evolutionary novelty. In these essays, he has a distinctly historical view that attempts to relate current data with the concerns of earlier generations of evolutionary and developmental biologists. In 2003, he had the honor to literally define "*evolutionary developmental biology*" in Hall and Olson's *Keywords and Concepts in Evolutionary Developmental Biology* (see Gilbert and Burian, 2003). Dr. Gilbert has received several awards and honors, including the Medal of François I from the Collège de France, the Viktor Hamburger Award from the Society for Developmental Biology of the USA and an honorary doctoral degree from the University of Helsinki. His research, which has been sponsored by the National Science Foundation and the John Simon Guggenheim fund, concerns the origin of that evolutionary novelty, the turtle shell. Most of the people in his laboratory are undergraduates at Swarthmore College.

The following interview is not a quoting of Scott's responses to a standard set of trivial personalized questions, although I could not avoid the latter completely. Rather, this is an extract from our numerous conversations and mutual commentaries on problems of developmental biology, always focused on how one might integrate the results from different developmental systems to provide fundamental insights into evo-devo. So we will try to pass some old and modern views on evo-devo research through the lens of Scott's long experience in the field. We are only hoping that at least a few stimulating views may be extracted from the material provided below. However, this paper is not only about evo-devo, but also about Scott's continuing life in science.

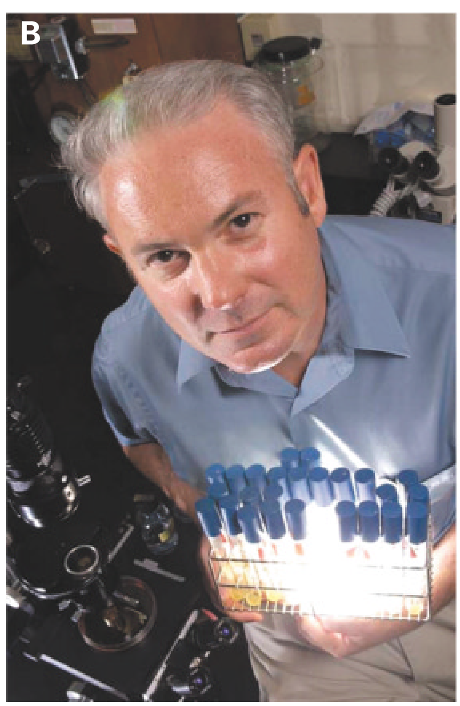
What and who motivated you to study embryology and when did you become interested in what we now term "evo-devo"?

I was thoroughly pre-adapted for the advent of evo-devo. During the summer after my sophomore year of college, I was privileged to be the teaching assistant of Dr. Michael Somers at an NSF [Ed. National Science Foundation]-sponsored program for high school students. He decided I needed to learn paleontology, so he had me bring the students to the lecture hall at 6:00 in the morning to learn it. I was also the teaching assistant in his evolution course for the college students, and he challenged me to take the developmental biology I was studying at Wesleyan University and to relate it to the big evolutionary questions I was studying during the summer. One day when I came into his office, he took his copy of *Science*, tore out an article and said, «*Explain this to me by tomorrow.*» It was the Britten and Davidson (1969) paper on the theoretical basis of gene regulation in eukaryotes. It became paper #1 of my reprint collection. When I returned for my senior year of college, this interest in relating evolution to development was further flamed by two books that I had purchased at a local used book store. The first of these books was Susumo Ohno's *Evolution by Gene Duplication* and the second was David DeGrood's monograph on Ernst Haeckel.

When I was a graduate student at Johns Hopkins University, I had hoped to work with Dr. Kirby Smith on the phylogeny of early chordates by looking at moderately repetitive DNA in tunicates, amphioxus and fish. I ran a lot of Cot curves, but Dr. Smith left the university and I found other advisors and other projects. However, my ideas about combining evolution and development received enormous support from an unexpected place. In addition to working in the laboratory of Dr. Barbara Migeon (who was pursuing her own synthesis of development and human genetics and who would later extend this work to include evolutionary ideas as well), I was also a masters degree candidate in the history of science department there. To be a biologist in the Johns Hopkins History of Science department in the early 1970s was an incredible experience, because three of the world's best historians of biology taught there then. So I took a tutorial on Sir Richard Owen from Camille Limoges, a course on Thomas Huxley from Bill Coleman and a seminar in the history of embryology from Donna Haraway. Dr. Haraway was writing her thesis on organicism in twentieth-century developmental biology and her course emphasized questions of polarity, organization and evolution. It was here that I learned about Waddington, Schmalhausen and others who had not been mentioned in the classes I was taking in modern developmental biology. I learned that there were questions involving the linkage of evolution and embryology that modern developmental biology had not asked for decades. So my early interest in evo-devo came more from my studies in history of science than from the science itself. In the late 1970s, when I was a postdoctoral fellow in the laboratory of that remarkable developmental biologist and musician, Bob Auerbach, Stephen Gould's *Ontogeny and Phylogeny* was published and Jacob's paper on tinkering came out. I felt like the field I was waiting for had just been born.

As mentioned, the field of evo-devo has emerged as a distinct area of biological research over the past decade. While evolution seems to be an unprogrammed non-repeating process, development is a predictable process repeated in each lifecycle. It has been suggested for a long time that for evolution to occur, developmental programs must change. Coincident with this assumption are a variety of both old and new conceptual issues regarding the evolutionary processes and the use of results from studies of development to make testable predictions about relationships existing between large animal groups. It is widely accepted that the roots of evolutionary changes in animal shape and form can be identified by studying the developmental mechanisms that control body pattern and shape in embryos. The discovery that the Hox transcription factors are fundamentally important during development and occur in most animal groups demonstrates that many key aspects of development are shared across taxa. For me, as an evo-devo fan, development contributes to evolution by identifying and dissecting of common developmental mechanisms that underlie the formation of functionally/structurally homologous features in distinct animal groups. In the broadest sense, such interpretation stems from von Baer's thoughts on development and evolution. Certainly, von Baer's embryology provided Darwin with the key element to explain homology and at the same time suggested that homologies were to be found more readily in the developing organisms than in the adult forms (see Mikhailov, 1997). However, other views on evo-devo approaches are also known. So the next question is as follows: in your opinion, what is evo-devo: "evolutionary developmental biology", "evolution of development" or "evolution and development"? Do these points of view have a common origin or are they separate lines of biological thinking?

I think that evo-devo is a fabric that contains many compatible threads. I think its main focus is how evolution arises and is constrained through developmental processes. Just as development is the link between the inherited genome and the phenotypically adult organism, so developmental processes are those needed to convert genetic changes into evolution. Kowalevsky's contemporary, Thomas Huxley (1893), said it succinctly, "*Evolution is not speculation but a fact; and it takes place by epigenesis*." The three



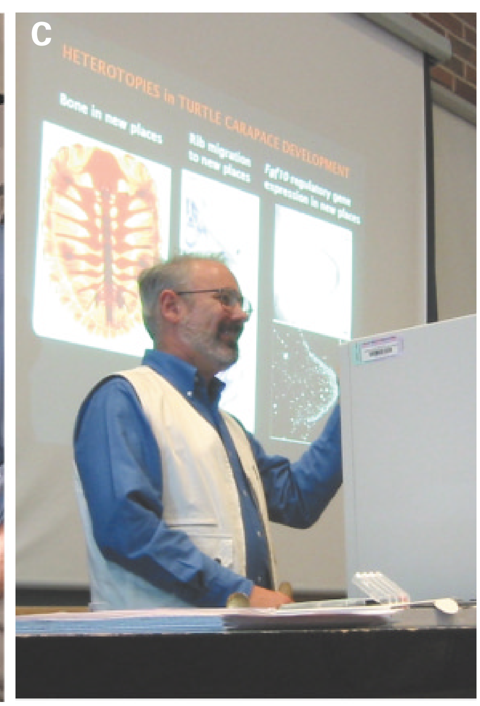


Fig. 2. Images which capture some moments from the scientific and teaching activity of Dr. Gilbert over the years. (A) *At the beginning of becoming an evo-devoist: Scott Gilbert (right) teaching biology at the program for high school students in 1969. Courtesy of Alan Levy.* **(B)** *Scott Gilbert in his laboratory, 2001. Photograph from Jim Graham.* **(C)** *How the turtle got its shell: the development of an evolutionary novelty. Scott's lecturing on the formation of the turtle shell (From the annual meeting of the Finnish Society for Cell and Developmental Biology, Hyytiälä, Finland, 2003).*

major subsets of this concern become: (1) how evolutionary novelty and stasis are produced through developmental interactions; (2) how development itself evolves and (3) how development can allow developing organisms to survive in particular environments. I don't think that these can be separated into different sciences, because they interact at so many levels and places. I think that these concerns had similar origins, since the science of the nineteenth century (and early Twentieth century) was so much less specialized than our own (see Gilbert 2003b). If one looks at the work of Kowalevsky, Metchnikoff, Severtsov, Schmalhausen and Waddington, one finds these three areas being worked on simultaneously. Metchnikoff and Kowalevsky, for example, both looked at the homologies which united the invertebrates and the vertebrates, and they also looked at how gastrulation (and the mesoderm) might have first evolved. Schmalhausen, Severtsov and Waddington looked at canalization and the production of evolutionary novelty, but they also looked at the roles that the environment played in phenotype production and how the organism might have evolved so that it could make plastic developmental responses to environmental changes. Although some scientists have proposed reasons for conceptually separating evo-devo, devo-evo and eco-devo, I think that evo-devo, "evolutionary developmental biology," should be the umbrella that brings them all together.

The discovery that the Hox transcription factors are fundamentally important during development and occur in most animal groups demonstrated that many aspects of development are shared across taxa. At the same time, a growing body of evidence indicated that the diversity of body plans across many phyla is not reflected in a similar diversity at the control (master) gene level. If the phenotype novelty that is observed comparing adults forms from different phyla is not always reflected in the sequences that control the shaping and morphogenesis of their embryos, where does it come from? A big question, therefore, for evo-devo research is how do novelties originate in evolution and where does the novelty come from?

Müller and Wagner (1991) have defined a morphological novelty as "*a new constructional element in a body plan that neither has a homologous counterpart in the ancestral species nor in the same organism.*" Novelty must represent a qualitative, rather than a quantitative departure. But by defining such innovations in terms of homology means that levels have to be specified. The neural crest is a major innovation because it is a cell type that had not been seen in evolution prior to the vertebrates. The turtle shell is an evolutionary novelty because it is a new structure that hadn't existed in other vertebrates, even though it is made of the same cell types that had existed previously. This latter form of evolutionary innovation comes from the tinkering that François Jacob (1977) had mentioned as being critical for evolution. Wallace Arthur (2004) notes that developmental novelties originate in four possible ways: altered timing (heterochrony), altered positioning (heterotopy), altered amounts (heterometry) and altered gene product (heterotypy). We have seen examples of each of these mechanisms; for instance, heterometry in the beaks of Darwin's finches, heterotopy in the bones of the turtle shell, heterochrony in the emergence of direct development in sea urchins and heterotypy in the Ultrabithorax protein that specifies the six-legged condition of insects. The deeper type of novelty—a new cell type, for instance—is more difficult to explain and probably will demand knowledge of entire groups of gene-protein interactions. However, the advances in computational modeling and genomics point to a time soon when we will be able to extrapolate how a neural crest cell or podocyte first emerged.

One may think that animals are so complex and their parts so interconnected that any change big enough to produce a new species would cause fatal failures. Homeotic mutations long seen to be the creative powers in evolution, but Goldschmidt's hopeful "monsters" or "monster-like" creatures do not seem to be viable. According to Sean Carroll (2000), the regulatory modules that were found in complex regulated genes can be possible targets for evolutionary divergence, because an organism may accommodate a new regulatory module without serious side-effects. How-

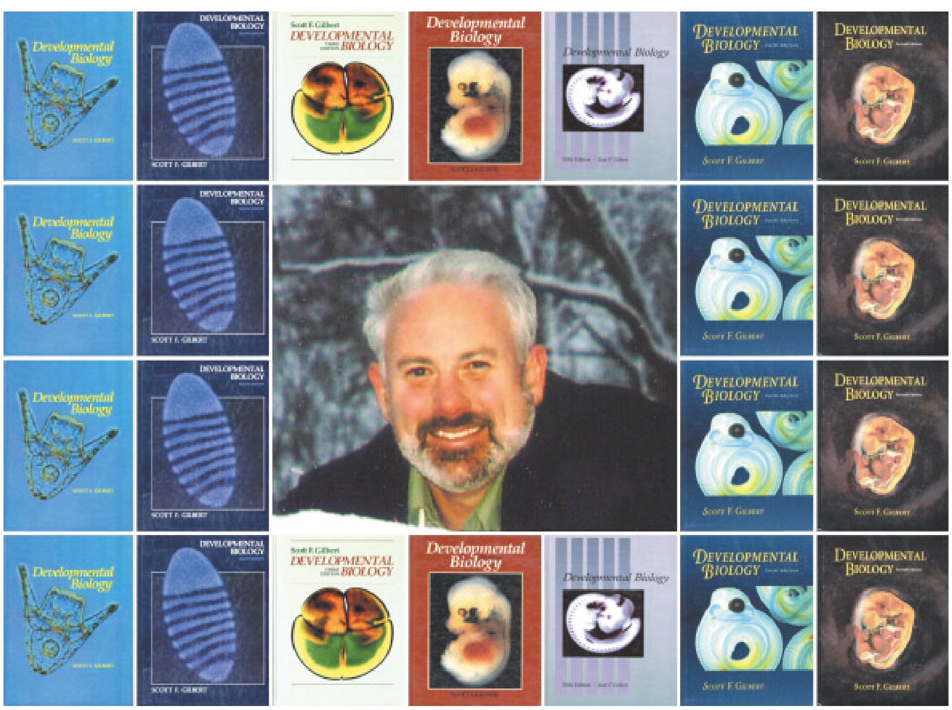


Fig. 3. Scott's landmark "*Developmental Biology*" book. First edition,1985: *Reprinted in Spanish (1987) and Italian (1988).* Second edition, 1988: *Reprinted in Japanese (1991) and Russian (1993).* Third edition, 1991: *Reprinted in Portuguese (1994).* Fourth edition, 1994: *Reprinted in French (1996).* Fifth edition, 1997. Sixth edition, 2000. Seventh edition, 2003: *Reprints being prepared in Japanese and Russian. (Collage by ATM and Mario Torrado; photo of Scott, courtesy of K. Lilleväli).*

ever, a change in a proper regulatory protein that controls a set of target genes in distinct embryonic tissues would be more difficult to accommodate. Rudolf Raff provides considerable insight into the problem by examine developmental molecular programs in hybrids obtaining from "crossing" of indirectly and directly developing sea urchins. Of note, the ontogeny of these hybrids is distinct from either parental species. The results indicated (Nielsen *et al.*, 2000) that such larva express genes derived from both maternal and paternal genomes in *de novo* created hybrid developmental settings. For me, these observations are particularly germane for shifting to the next question: Do these and other available results mean that it will be difficult or even impossible to deduce the developmental functions of a given control gene based exclusively on its structure and molecular function without accounting for cell settings where the gene works?

I think that one of the most important discoveries in recent developmental genetics has been the context-dependent actions of regulatory genes. Even *Pax6*, so essential for eye determination, is also needed for the differentiation of the endocrine pancreas and the pancreatic ducts. In the context of other head-associated transcription factors (*Sox2, Maf, etc.*) Pax6 helps form the eyes, but in the presence of gut-associated transcription factors (*Pbx1, Pdx1, etc*), it is required for pancreatic development. Thus, a tissue expressing *Pax6* is not "destined" to become an eye. Rather, the developmental history of the cell is important. Similarly, the paracrine factor BMP4 has different activities depending on the field in which it is secreted. In the early vertebrate embryo, it specifies epidermis. In the limb field, it specifies digit identity. In later limb, it is critical for ossification and in the autopod, it causes the apoptosis of the interdigital webbing.

Studies in evo-devo are now providing evidence that the modularity of enhancers allows regulatory genes to be utilized in different places (the Boolean "or" condition) such that mutations in one of these enhancer modules can lead to a specific phenotypic change without causing alterations in the entire organism. The *bmp4* expression patterns in the beaks of Darwin's finches can change without concomitant changes in *bmp4* expression elsewhere and *Pitx1* expression in the aquatic three-spine stickleback fish can be lost in the pelvic region without affecting the neuromasts and thymic cells in which this gene is also expressed. These are most likely due to mutations in specific enhancer sequences.

One question more about recent findings on how the same control gene can act in different developmental settings in non-related species. One such gene, the *Pax6* gene, comes close to exhibiting the effects expected of a universal "master" control gene for eye development. Mutations in *Pax6* in mammals and insects prevent eye development, whereas its targeted expression is capable of inducing ectopic eyes in non-eye tissues (see Gehring, 2004). Would you agree with the assumption that a master control gene can instruct target cells and can, therefore, redesign the body plan or it can only re-direct differentiation of relatively small cell groups?

Powerful things must be powerfully controlled. So "master regulatory genes" are among the most masterfully regulated genes we know. Moreover, not every cell can respond to such a gene. Rather, the field or module that the cell is in plays a major role. For instance, *Pax6* can only activate eye development in those cells meeting the preconditions for forming eyes. Hedgehog and Wingless signaling is required for the ectopically expressed *Pax6* gene to specify eyes in *Drosophila* and the *eye gone* gene appears to be needed independently of the *Pax6* gene in order to coordinate eye differentiation and

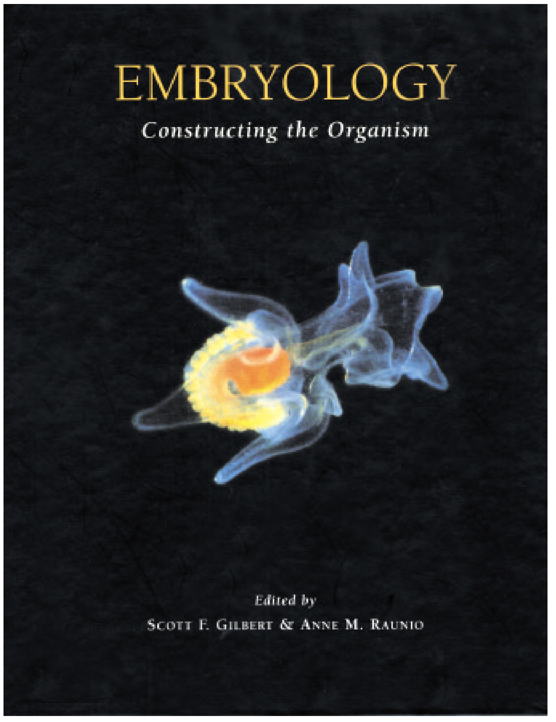


Fig. 4. Cover of the book *"Embryology: Constructing the Organism" by S.F.Gilbert and A.M. Raunio, 1997.*

growth (see, for example, Jang *et al.*, 2003; Dominguez *et al.*, 2004). Therefore, I think that these master regulatory genes (I'd rather call them "eye specification genes") can only work in certain morphogenetic fields wherein the preconditions are already met. I suspect that there is a strong selection for such regulatory systems, so that transdetermination does not routinely occur.

The discovery of homologous regulatory genes for analogous structures (such as the vertebrate and insect eyes) was one of the first discoveries of evolutionary developmental biology (see Gilbert *et al.*, 1996). The existence of homologous genes in distantly related species was not given credence by classical evolutionary biologists until these discoveries. Amundson (2005) notes that until then evolutionary biologists thought that similarities would be brought about through selection and not by common descent.

My next questions are more personal. Perhaps no one has contributed as much to teaching embryology, developmental biology and evo-devo as Scott Gilbert. I am referring to the famous textbook *Developmental Biology.* Reading its 7th edition, one can note that once more Scott was able to put modern concepts and ramifications of developmental biology into language equally understandable for both students and researchers. Your book, "Developmental Biology", was first published

in 1985. Really, it must be very difficult to keep such a textbook up to date with modern science. Writing the book at first and then re-writing it several times to prepare it for further editions, was it your aim to generate a common sense regarding "laws" and "principals" of developmental biology or was it to transmit adequately well-documented information about developmental processes in various model organisms?

First, thank you for the very kind words. I don't think we will ever have "laws" the way physicists do and this is largely due to the evolutionary nature of development. What works in one species does not necessarily work in another. Marilyn and David Kirk (2004) have recently written that *Volvox carteri* turns out to be an excellent model system for the development of other *Volvox carteri*. Not even other Volvoxes develop the same way! Kowalevsky's motto was "*In specialibus generalia quaerimus — We seek the generalities in the specifics*." I think that this is what we can aspire to do and that is what the textbook attempts.

The first edition of the textbook was written as an attempt to integrate (indeed to celebrate) the organismal, cellular and molecular approaches to animal development. A new feature of the book, the Sidelights and Speculations sections, allowed me to add ecological and environmental approaches too. Thus, I was able to have sections on such topics as "Development and Macroevolution", "Environmental sex determination and extinction", "Heterochrony", "Neoteny" and "The Control of Insect Development by Plant Precocenes". Indeed, in the preface to that (1985) edition, I wrote that: "*this book attempts to blur some of the lines separating developmental biology, genetics and evolution… Genetic mutations affect evolution by working through development and the elucidation of the mechanisms by which this is accomplished promises to be one of the most exciting chapters of modern biology.*" Evolutionary developmental biology received its own specific chapter in the third (1991) edition and the ecological approach is brought together in its own chapter in the fifth edition (1997).

The book is filled with author's interpretations of "mountains" of observations accumulated by experimental embryology and molecular developmental biology, testable hypotheses and suggestions. It moves a reader away from usual model organisms to the richness of comparative embryology, evo-devo, ecological aspects of development (i.e., eco-devo) and other ramifications of developmental biology, but always upon disciplined and solid arguments. However, what other topics do you like to write about, apart from your landmark "Developmental Biology" book ?

I actually enjoy writing lectures. Leonard Bernstein said that he loved Mahler's work and he loved his audience. Therefore, he wanted his audience to love Mahler's work as much as he did. I feel this way about developmental biology: I want my students to love it as much as I do. So writing a lecture allows me the opportunity to try to transmit this enjoyment, love and enthusiasm to my students. Besides, nature gives developmental biologists the best material to talk about. There are very few "crimes against nature", but making developmental biology boring must be one of them! I also enjoy writing science fiction and someday I hope to have the time and nerve to actually complete one of these stories.

Scott's contributions to developmental biology extend far beyond his own published research. Scott's knowledge of the historical roots of embryology makes him a popular speaker on the subject of evolution and creationism. But faith is perhaps more of a personal, rather than a professional "skill". For instance, von Baer was a believer, and he was an excellent scientist, really a Renaissance man. It is true that von Baer's embryological research did not serve the purpose that he intended. Rather than proving the Bible right, Baer's embryological observations led to the birth of comparative embryology which served as background for moving toward evolutionary embryology that culminated in evo-devo exploring. Does this mean that a firm faith is compatible with a strong biological background?

Here is another example of context dependency. In von Baer's time religious belief was often the motivation for good scientific research. Under the rubric of "Natural Theology", the world was viewed as God's creation and therefore provided evidence for the goodness, power and wisdom of the Creator. By studying the natural world, one could gain knowledge of the how God worked. Indeed, the more mechanical and intricate the details of his creation, the more glory accrued to its Creator. Religion was the starting point for excellent science. Today, however, if one reads *Genesis* literally (which is impossible, since there are numerous contradictions in the book and these demand interpretations), then evolution must be false. (Evolutionary developmental biology now has some of the best evidence with which to counter Creationism, see Gilbert, 2003c).

However, one can still be a religious person and do good science, but one has to interpret the Bible and not see it as a science textbook for the ancient Hebrews. For instance, Maimonides, the great Twelfth century rabbi, said that a pious man of his day believed that in every pregnancy an angel of God entered into the uterus and molded the material there into an embryo. This, these men would claim, is a miracle. How much more a miracle would it be, continued Maimonides, if God had so made matter that it could form an embryo without angelic intervention at each pregnancy. Just as we believe that matter can form an embryo without divine power, it seems natural (especially from the evo-devo viewpoint which sees evolution as coming from changes in development) that a religious person can also believe that God had created matter in such a way that it can evolve without divine supervision. God wouldn't have to preside over the speciation of the black-throated blue warbler and the black-throated green warbler (as well as getting them to and from Noah's ark along with the 750,000 known species of insects).

There is a second approach to science and religion, as well. As the philosopher Abraham Heschel has noted, both religion and science claim to be grounded in the experience of "wonder." But wonder, Heschel continues, decays rapidly into curiosity and awe. From curiosity we get science and philosophy, from awe we get reverence and religion. Thus, science and religion are like cousins with a common grandparent (and can be allied in the preservation of the sources of wonder). Embryos continually expose us to wonder and wonder remains an operative category in developmental biology. (Indeed, reviewers of developmental biology textbooks will say whether or not the author has captured

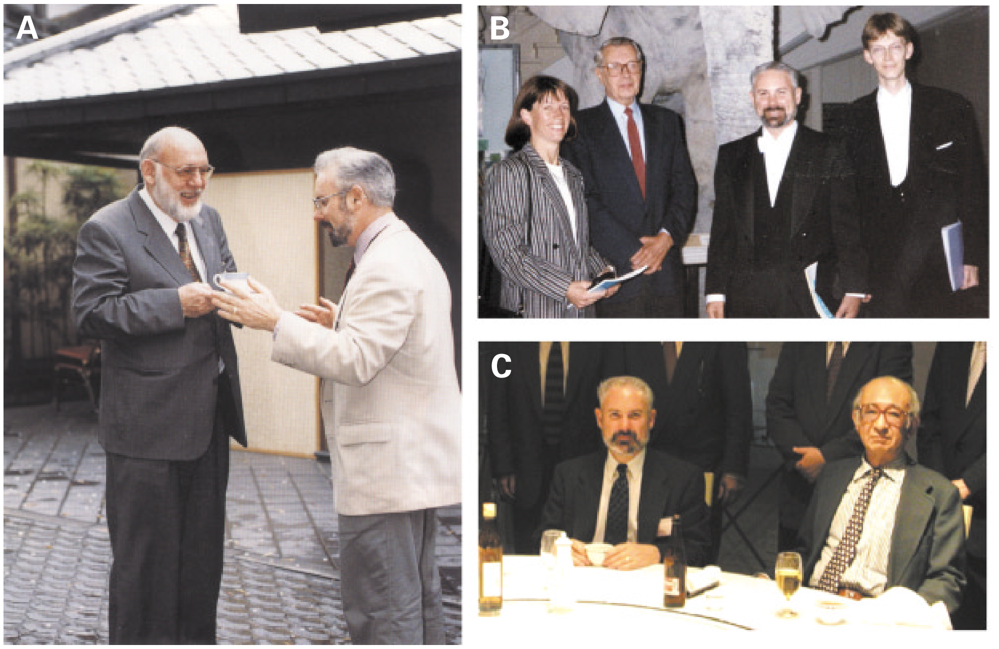


Fig. 5. Scott Gilbert with some representative developmental biologists from various countries. (A) *With Walter Gehring (left) at the Taniguchi Symposium on Developmental Biology IX ("Developmental Biology in Half a Century") in Kyoto (1997).* **(B)** *At the University of Helsinki. From left to right: Irma Thesleff, Lauri Saxén, Scott Gilbert and Jukka Jernvall just after Jernvall's thesis defence. Dr. Gilbert was the "opponent" for Jukka Jernvall's thesis defence.* **(C)** *With Tokindo Okada (right) during the Japanese Society for Cell and Developmental Biology meeting in Yokohama (2002).*

the wonder of the developing organisms). So it is not surprising that many developmental biologists combine a materialistic view of science with a respect for the wonder of what they see (see Gilbert and Faber, 1996).

Since you have now had time to reflect upon your work in evo-devo, what generalizations can you make?

I am constantly reminded how similar educational development is to embryonic development. First, the early inductions give one the competence to respond to later signals and who you meet and who teaches you is critical. (And here I have just been incredibly lucky!). The role of personality and being at a particular place is amazingly important. Second, I have been impressed by the role of signaling in the «maintenance» as well as establishment of phenotype. Becoming an evo-devoist does not mean remaining one if you do not have a supportive environment. In this, my family and Swarthmore College have given the «permissive conditions» to become a proponent and practitioner of evo-devo and Andy Sinauer and Carol Wigg are responsible for getting that textbook out every three years. Instructive interactions to continue on this path were given by a series of informal teachers including such pioneers as Jack Berrill (who retired to Swarthmore), Paul Maderson, Tokindo Okada and John Opitz. I also had the opportunity of learning from (and bouncing ideas off of) such remarkable collaborators as Jessica Bolker, Dick Burian, Lauri Saxén, John Fallon, Rocky Tuan, Mary Tyler, John Opitz, Kirsi Sainio, Rudy Raff, Sahotra Sarkar, Annie Burke, Beth LeClair, Grace Loredo and Mark Harris. Judy Cebra-Thomas has been especially important both as collaborator and as a superb colleague at the college. Third, community effect plays a major role in sustaining the phenotype. For me this consists of the community of students and faculty at Swarthmore College as well as the far-flung informal community of fellow evo-devo people whose signals form a major substructure in my e-mail boxes. These include Gerd Müller, Brian Hall, Fritson Galis, Shigeru Kuratani, Yoshiko Takahashi, Fred Nijhout, Patricia Hernandez, Sean Carroll, Greg Wray, Billie Swalla, Jukka Jernvall, Irma Thesleff, Ron Amundson, Manfred Laubischler, Jason Roberts, Günter Wagner, Alexander Mikhailov, Lien van Speybroeck and Cor van der Weele. This community not only supports mutual differentiation and patterning; it also prevents apoptosis. I feel nowhere near the end of my career and I hope I can live up to this honor. I sincerely thank the nominating committee and the scientific Council of the St. Petersburg Society of Naturalists for this wonderful honor and vote of confidence.

You have obviously made a most enormous contribution to evo-devo, but I have the feeling that your scientific interests will never wane. Well, Scott, we'll have to close this discussion which has been fascinating. Thank you very much for sharing your thoughts with us.

Summary

This article announces Dr. Scott F. Gilbert as the winner of the Alexander Kowavelsky international prize (2004) and briefly reviews his achievements in developmental biology and evo-devo. Dr. Gilbert replies to the interviewer's questions concerning his personal interest in evo-devo and current controversies within the field. His thoughts and comments represent a unique blend of research talents and skills, curiosity and creativity.

KEY WORDS: *evo devo, Kowalevsky Medal, Scott Gilbert*

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