ALTENBERG SEMINARS IN THEORETICAL BIOLOGY

Summer 2006:
Evolutionary Developmental Biology

Hörsaal 1, Biozentrum, Althanstrasse 14, at 6.15 p.m.

The Program at a glance:

9 March 2006
Stuart A. NEWMAN (New York Medical College, Valhalla, NY, USA):
"Physical Determinants of Metazoan Form and the Molecular Homology-Analogy Paradox"

27 April 2006
Adam S. WILKINS (Editor, BioEssays, Cambridge):
"Evolutionary Genetics, Genomics, Genetic Networks: How Should We Approach the Genetic Foundations of the Evolution of Development/Morphology?"

1 June 2006
Frietson GALIS (Leiden University):
"The Evolutionary Conservation of Body Plans: Internal Selection, Pleiotropy, and Homeobox Genes"

22 June 2006
James R. GRIESEMER (University of California, Davis):
"Variational Models for Developmental Processes: A New Ontology for Evo-Devo"

29 June 2006
Rudolf A. RAFF (Indiana University Bloomington, USA):
"Mechanisms of Radical Evolutionary Changes in Larval Morphology"

The topic

Embryology played an indispensable role in the first inceptions of evolutionary theory by Charles DARWIN, August WEISSMAN, Ernst HAECKEL, and others. Yet embryology — which more recently came to be called developmental biology — was conspicuously absent from the Modern or Evolutionary Synthesis. Evolutionary biology was built on a huge black box; and maybe, as is sometimes suggested, rightly so: " DARWIN could never have written the Origin of Species if he had not wisely bracketed the mechanism of inheritance" (AMUNDSON 1994). Similarly, it is often seen as a great advantage of Mendelian genetics in the early decades of the 20th century that it "bypassed the uncharted swamp of development" (David HULL). The disrepute of Haeckelian recapitulationism as well as neo-Lamarckian beliefs about environmental influences on embryogenesis, which many developmentalists continued to advocate, contributed to this ostracism.

In the past two decades or so developmental considerations have come to the fore again, stimulated by the rise of molecular developmental genetics (RAFF 1996; HALL 1999; DAVIDSON 2001; GILBERT 2003; CARROLL ET AL. 2004), and motivated by a number of explanatory deficits in the prevailing evolutionary paradigm. The field that embraces studies of embryonic development as the vehicle for evolutionary change is called evolutionary developmental biology ("EDB" or "EvoDevo"). EvoDevo forges a synthesis of mechanisms that operate during ontogeny with those that operate during phylogeny (between generations). Brian K. HALL (2000) characterizes EvoDevo as a way of integrating proximate and ultimate causes for the origin of phenotypes. As the empirical and theoretical analysis of the causal-mechanical connection between embryological/developmental and evolutionary processes, EvoDevo is immanently dialectical: on one hand, it is interested in the factors that together explain the "origination" of ontogenetic systems and the mechanisms that account for their subsequent modification, suppression, or loss (MÜLLER and NEWMAN 2003); on the other, it investigates the ways in which the properties of ontogenetic processes influence the course of morphological evolution (cf. GILBERT ET AL. 1996; RAFF 2000).

Concepts that help delineate EvoDevo from more established research in developmental biology and evolutionary biology include body plans, combinations of morphological characters of a taxon that have been unusually conserved during evolution (GALIS seminar); canalization, the reduced sensitivity of a phenotype to changes or perturbations in the underlying genetic and nongenetic factors that determine its expression; constraints, processes or mechanisms that limit the ability of the phenotype to evolve or bias it along certain paths (GALIS seminar; cf. AMUNDSON 1984); evolvability, the inherent potential of certain lineages to change during the course of evolution; and modularity, which views organisms as the integration of partially independent, interacting units at several hierarchical levels (RAFF seminar). Three concepts that we take to be pivotal for EvoDevo — evolutionary origination, innovation, and novelty — will be highlighted in particular in NEWMAN's seminar. Comparative developmental biology, experimental developmental biology, and evolutionary developmental genetics are the methods most commonly relied on in EvoDevo.

From an epistemological point of view, what current EvoDevo seems to be largely lacking is a way to get from the knowledge of parts (entities and their properties) and what they do to each other — "local knowledge" that developmental genetics increasingly provides — to a full-fledged, formal explanation of developmental phenomena. Developmental genetics begins with an induced anomaly (a mutation) and a (hopefully discrete) consequence, then proceeds to decipher a "perturbation-to-consequence chain" — a kind of account that "doesn't articulate any sense of the mapping from genotype to phenotype, which is what we ultimately want" (VON DASSOW and MUNRO 1999). COFFMAN (2006) proposes that during immature stages with relatively low specification and high potential, development is largely controlled by local interactions from the "bottom-up," whereas during more highly specified stages with reduced potential, emergent autocatalytic processes exert "top-down" control ("developmental ascendency").

The explanatory strategy Stuart NEWMAN will explore in his seminar focuses on the epigenetic factors that are causal in the evolution and organization of phenotypes. Here the generic physical properties of cells and tissue masses and their self-organizational properties are given priority over the molecules that are used in these processes. His picture implies two evolutionary regimes in the history

of multicellular life: an early, "pre-Mendelian" phase in which physically mediated plasticity prevailed and in which a given genotype corresponded to a multiplicity of morphological phenotypes, and the current, advanced, "Mendelian" phase in which determinate morphological phenotypes are brought about by hierarchically organized genetic programs.

Adam WILKINS's seminar will focus on the divergent viewpoints about the kinds of genetic change that are most important in developmental evolution as embodied in evolutionary genetics, genomics, and the "network thinking" of systems biology, and propose a synthesis. The most difficult task ahead, WILKINS contends, is the synthesis of "physicalist" (causal-mechanistic) and informational (genetic) approaches, a topic that will also be addressed by GRIESEMER.
Frietson GALIS will report on her studies of fetal deaths in humans, which suggest strong internal selection against variation of body plan characters by deleterious pleiotropic effects. Her hypothesis is that the strong interactivity during the patterning of the embryonic axes causes the conservation of body plans.
The core idea in the "reproducer perspective" which Jim GRIESEMER has been developing in the last decade is material overlap: offspring form from organized parts of parents, such as cells, rather than by the copying of traits. GRIESEMER will develop a process perspective on the relations between reproduction and development that allows to study developmental processes by means of variational models, taking into account deep connections between heredity and development instead of relying on the reductionist informational picture.

Rounding off this seminar series, Rudolf RAFF (who, according to the developmental biologist and historian Scott GILBERT, "is accomplishing a resynthesis of the entire field of biology — nothing less") will show that the evolutionary modification of various processes in ontogeny, including oogenesis, cell fate specification, axis formation, and morphogenesis are accessible to experimental study at the level of gene action in sea urchins.

Ranging from experimental to theoretical and even philosophical work, these seminars will offer a quite representative sample of ongoing work in EvoDevo.
Will EvoDevo contribute to an Extended Evolutionary Synthesis? Generation after generation, biologists have hoped that at long last embryology was reaching a stage of theoretical maturity that would permit a major new synthesis. This time they may be right.

References

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Abstracts and biographical notes

Stuart A. NEWMAN
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Physical Determinants of Metazoan Form and the Molecular Homology-Analogy Paradox

9 March 2006

Abstract

The neo-Darwinian solution to the problem of organismal evolution confronts challenges on several fronts: (1) the fossil record is deficient in transitional forms between many major innovations, and it is rare for there to be plausible gradual developmental mechanisms to get from one form to another embodying an innovation (e.g., from an unsegmented to a segmented worm); (2) new forms appear rapidly and remain evolutionarily stable for long periods, e.g., the burst of body plans that preceded the Burgess Shale deposits of ~540 million years ago; (3) the rate of gene mutation is discordant with the rate of morphological evolutionary change in numerous phylogenetic lineages, and many genes centrally involved in morphogenesis in modern organisms can be eliminated in knockout experiments without compromising the developmental outcome; (4) mutations of "large effect" are now known to have contributed to evolutionary change in plants and have even been fixed in animal populations; (5) morphogenesis of many non-metazoan and some metazoan forms is highly plastic and environmentally-conditioned, suggesting that the programmed, determinate development of animal embryos may be an exceptional property of multicellular organisms, a product of evolution rather than its precondition.

A body of information acquired over the past decade which illustrates these problems in a particularly vivid fashion is the conservation of the "developmental-genetic toolkit," a small number of intracellular and extracellular signaling molecules and transcription factors that originated with the metazoa and underlie virtually all morphological processes in modern animals. This has led to the paradox that analogous features of body plans and organ forms in distantly related animals (e.g., segmental organization and eyes in arthropods and vertebrates) can be homologous at the molecular level.

Many of these difficulties for evolutionary theory can be resolved by relinquishing the strict genetic determinism underlying the standard model. Consideration of cell aggregates, such as those leading to modern multicellular organisms and those of the primordia of organs such as the paired limbs of tetrapods, as chemically active physical materials, shows them to be susceptible to epigenetic formative principles with a wide range of interconvertible morphological outcomes. Rapid organization and reorganization of morphology in response to environmental or small genetic changes would thus be the expectation for all multicellular forms, especially during early phases of evolution. In some lineages, including those leading to the modern metazoa, subsequent selection for integration, stabilization, and fine-tuning would have produced the determinate, evolutionary static, species-characteristic developmental systems of modern animals. This picture implies two evolutionary regimes in the history of multicellular life: an early phase in which physically mediated plasticity prevailed and in which a given genotype corresponded to a multiplicity of morphological phenotypes, and an advanced phase in which determinate morphological phenotypes are brought about by hierarchically organized genetic programs. These two phases would be realized to different extents in different phylogenetic lineages and separated by evolutionary periods in which the modes are mixed. The neo-Darwinian framework of incremental evolutionary change is most pertinent to organisms of the advanced phase; macroevolution and large-scale cladogenesis is characteristic of the early phase.

Biographical note

Stuart A. NEWMAN (AB 1965, Columbia, PhD chemistry, 1970, University of Chicago) is a professor of Cell Biology and Anatomy at New York Medical College, Valhalla, NY. He has contributed to several scientific fields, including biophysical chemistry, developmental biology, and evolutionary theory. He has held faculty positions at the State University of New York at Albany and the University of Pennsylvania, and was a visiting research fellow at the University of Sussex, UK, an INSERM Fellow at the Pasteur Institute, Paris, a Fogarty Senior International Fellow at Monash University, Australia, and a visiting scientist at the University of Paris-Sud, the French Atomic Energy Center-Saclay, the Indian Institute of Science, Bangalore, the KLI, and the University of Tokyo. Dr. NEWMAN was a founding member of the Council for Responsible Genetics (Cambridge, MA) and is currently a Fellow of the Institute on Biotechnology and the Human Future (Chicago, IL).

Selected publications

(2006) The developmental-genetic toolkit and the molecular homology-analogy paradox. Biological Theory 1, in press.
(2005) Biological Physics of the Developing Embryo (with G FORGACS). Cambridge UP.
(2004) Dynamical mechanisms for skeletal pattern formation in the vertebrate limb (with HGE HENTSCHEL, T GLIMM, and JA GLAZIER). Proceedings of the Royal Society London B271: 1713—1722.
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Adam S. WILKINS
Editor, BioEssays

Evolutionary Genetics, Genomics, Genetic Networks: How Should We Approach the Genetic Foundations of the Evolution of Development/Morphology?

27 April 2006

Abstract

The goals of EvoDevo as a field are to understand the mechanisms, processes, and patterns of evolutionary change in developmental change, which have been responsible for the immense diversity of animal and plant forms that have arisen on Earth during the past 550 million years. Successful completion of the "task" of the field, however, will depend, in part, on advances in understanding in developmental biology itself, in particular of the processes of morphogenesis and how these processes relate to their underlying informational (genetic) foundations. Within the domain of EvoDevo itself, however, lies another distinct challenge — understanding the nature of the genetic changes that are intrinsic to the changing patterns of form – shape, size, and color patterns — that constitute the diverging morphological sequences in different lineages. Since a vast amount is known about mutational processes, in both formal genetic and detailed molecular terms, this might seem to be relatively easy to resolve. It is not, however, because there are, in reality, some strong divergences in viewpoint about the kinds of genetic change that are most important in developmental evolution. These different viewpoints are embodied in three distinct fields, with their own distinctive approaches: evolutionary genetics, genomics, and systems biology — the latter devoted to what can be called "network thinking."

In this talk, I will discuss these different approaches and their respective strengths and limitations. I will argue that "network thinking" is the critically important approach but that it, too, will be inadequate unless it incorporates key elements of the other approaches. A critical challenge for the field will be effecting that synthesis. In the penultimate part of the talk, I will discuss three evolutionary problems where the network perspective in itself deepens understanding of the issues — even in the absence of detailed knowledge of any specific genetic networks involved. And, in the final part, I will return to the ultimate and still most difficult task ahead, the needed synthesis between "physicalist" and informational (genetic) approaches if we are to understand morphogenesis and the evolution of morphogenetic processes.

Biographical note

Adam S. WILKINS has been the Editor of BioEssays, a review journal specializing in molecular, cellular and developmental biology (now published by Wiley) since January 1990, after having been the journal's Staff Editor at Cambridge UP from 1984 to 1989. Dr. WILKINS studied Biology at Reed College, Portland, Oregon (BA, 1965) and genetics at the University of Washington, Seattle (PhD, 1969). He held postdoc positions in MIT's Department of Biology (1969-1973), where he worked in phage molecular genetics, and in the McArdle Laboratory for Cancer Research, University of Wisconsin, Madison, where he was involved in research on slime mould genetics, cell biology, and developmental biology. Dr. WILKINS was a Lecturer and Senior Lecturer in Genetics at Massey University, Palmerston North, New Zealand (1976-1983), and a Visiting Professor in the departments of genetics at the University of Washington, WA (1985), and the University of Wisconsin, Madison (1987 and 1993). He also held a Visiting Lectureship at the Department of Biochemistry, The National University of Singapore (1994).

Selected publications

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(2005). The molecular elements that underlie developmental evolution (with CR ALONSO). Nature Reviews Genetics 6: 709—715.
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Frietson GALIS
Institute of Biology
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The Evolutionary Conservation of Body Plans: Internal Selection, Pleiotropy, and Homeobox Genes

1 June 2006

Abstract

Body plans are those combinations of morphological characters of a taxon that have been unusually conserved during evolution. Yet, a) even the highly conserved characters of body plans virtually always display minor intraspecific variation, and b) new mutants with major effect on those characters are common. This suggests that the evolutionary conservation of body plans is usually caused by stabilizing selection.
Our studies on fetal deaths in humans indeed show strong internal selection against variations of body plan characters. The selection against variation appears to be caused by deleterious pleiotropic effects. Examples are the conservation of the number of cervical vertebrae and digits.

Many conserved characters of the vertebrate body plan are determined during the conserved early organogenesis stage. The cause for the conservation of the stage appears to be that mutations with an effect during this stage almost invariably lead to deleterious pleiotropic effects.

Because many adult traits are determined during early organogenesis, early developmental events have a persisting influence. My talk focuses on how such projected effects constrain the power of natural selection in shaping adaptive evolution. Our hypothesis is that the strong interactivity during the patterning of the embryonic axes is the cause of the conservation of body plans. Due to this interactivity, positive mutational changes of some character cause so many negative pleiotropic effects elsewhere that they are nearly excluded (so-called internal selection).

In a meta-analysis of the literature we have identified specific couplings between the A-P patterning of the mesoderm determining the number of cervical vertebrae and other patterning and morphogenetic processes. The multiple, correlated abnormalities that we found in human fetal deaths can be understood as resulting from such couplings.

The data show that applications of the concepts of evolutionary constraints and pleiotropy provide a novel insight into medical risks associated with seemingly harmless anatomical variations, such as cervical ribs and supernumerary digits.

Biographical note

Frietson GALIS completed her PhD in the Institute for Evolutionary and Ecological studies at Leiden University with an interdisciplinary study (1991). She did postdoctoral research at Wageninge and Leiden universities, and was a Fulbright junior scholar at Harvard University in 1993. She is now an associate professor in the Department of Theoretical Evolutionary Biology at Leiden University.

Her research focuses on innovations and mechanisms that facilitate evolutionary changes and on the constraining effect of internal selection on evolutionary changes (i.e., selection caused by characteristics of the developmental system). One project is on the conservation of the number of cervical vertebrae and digits in mammals. A second project concerns the role of phenotypic plasticity and genetic assimilation in the process of adaptation and evolutionary change of a cichlid fish. A third project concerns the intra-specific relationship between size and longevity in dogs.

Selected publications

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James R. GRIESEMER
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Variational Models for Developmental Processes: A New Ontology for Evo-Devo

22 June 2006

Abstract

It is often argued that models of evolution describe changes in population-level variation due to processes such as natural selection while models of development concern transformational processes within individual organisms. I sketch a process perspective on the relations between reproduction and development that bridges this divide and suggest ways to characterize and model developmental processes that are integrative rather than reductionist, taking into account deep connections between heredity and development rather than explaining all developmental processes in terms of genetic units. Historical and contemporary examples from developmental biology and evolution illustrate the new process ontology in contrast to the traditional one based on a hierarchy of genetic units.

Biographical note

James R. GRIESEMER has been a Professor in the Department of Philosophy at the University of California, Davis since 1996. He holds an AB in Genetics from the University of California, Berkeley (1977), an MS in Biology from the University of Chicago (1981), and a PhD in Conceptual Foundations of Science from the University of Chicago (1983). He joined Davis in 1983 after having been a researcher at the Museum of Science and Industry in Chicago (1981). He is an affiliate of the Center for History and Philosophy of Science of the California Academy of Sciences, and has been a fellow at the Wissenschaftskolleg zu Berlin (1992-93), the Collegium Budapest/Institute for Advanced Studies (1994-95), and the Max Planck Institut für Wissenschaftsgeschichte in Berlin (1998).

Selected publications

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Rudolf A. RAFF
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Mechanisms of Radical Evolutionary Changes in Larval Morphology

29 June 2006

Abstract

Despite the fact that all of the later stages of ontogeny of any animal are based on the events of embryonic and larval development, these early stages of development can evolve rapidly and dramatically among closely related forms. Larval development is relatively simple morphologically and in terms of gene regulation compared to adult development, which allows relatively rapid evolution to occur. In addition, the simpler larval systems lend themselves to more straightforward investigation. Basal sea urchin development is via a feeding pluteus larva. Direct development, in which feeding structures are lost and development to metamorphosis is accelerated, is derived. In Heliocidaris erythrogramma, direct development has evolved in less than 4 x 106 years since its divergence from H. tuberculata, which has a feeding pluteus. Although the H. erythrogramma larva appears simpler in form than the pluteus, it is in fact equally complex in process and structure. The evolution of direct development in H. erythrogramma involves a series of modifications to various processes in ontogeny, including oogenesis, cell fate specification, axis formation, and morphogenesis. These evolutionary changes are accessible to study experimentally at the level of gene action, and we have been able to demonstrate that at least one gene is responsible for a large effect on morphogenesis. Despite the enormous differences in ontogeny, it is possible to make viable cross species hybrids that have a novel ontogeny and yet metamorphose into sea urchins. The hybrids have allowed us to investigate gene interactions, and to focus on gene regulatory changes. We have found that evolution is faster in the H. erythrogramma lineage than in indirect developers. Evolution has largely involved changes in modular units. Most changes involve gene expression heterochronies, but there are module fusions, losses of localized gene expression patterns, gene losses, and gene co-options as well.

Biographical note

Rudolf A. RAFF is James H. Rudy Professor of Biology and Director of the Indiana Molecular Biology Institute, College of Arts and Sciences, University Graduate School, Indiana University, Bloomington. He served as a Navy lieutenant, was instructor-in-chief of the Summer Embryology Course at the Marine Biological Laboratory at Woods Hole, and founded the Indiana Molecular Biology Institute at Indiana University in 1983. Dr. RAFF is co-founder and editor-in-chief of the journal Evolution and Development and has served as an associate editor for several other journals; he is also a member of the editorial board of Biology and Philosophy. He has been invited to lecture widely — recently at the University of Chicago, Duke University, the University of Toronto, the Pasteur Institute in Paris, and a public lecture sponsored by the city of Aomori in Japan. Since 1986, he has been an annual visiting scholar at the University of Sydney, Australia.

Awards that RAFF has received include fellowships from the National Institutes of Health, the American Cancer Society, and the Guggenheim Foundation. He won the 2001 Kowalevsky Medal and was elected to the American Academy of Arts and Sciences in 2000.

Selected publications

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