

24th ALTENBERG WORKSHOP IN THEORETICAL BIOLOGY

***Biological and Physical Constraints on
the Evolution of Form in Plants and Animals***

organized by

Jeffrey H. Schwartz and Bruno Maresca

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Konrad Lorenz Institute

for Evolution and Cognition Research

Altenberg, Austria

Topic and aims

Although the comparative study of morphology has for centuries been a viable intellectual pursuit, inquiry into the emergence of the form or shape of structures under scrutiny still often remains a disconnected endeavor. For example, during the 1970s and especially 1980s the guiding principle was Lewis Wolpert's "pattern formation" model, in which the focus was on positional information and variation in what William Bateson referred to as "repeated parts." For developmental biology, the notion of naïve cells being imbued with the potential to generate structure and form from an extrinsic morphogenetic source was challenged by the perspective that the emergence of structure and form was at least as much due to properties intrinsic to cells and between cells in time and space.

Later in the 1980s and into the 1990s, the discovery in animals and then plants of homeobox genes and their roles in both generating positional information and affecting the development of repeated parts seemingly opened up new vistas for understanding morphology and its use in systematics and phylogenetic reconstruction. For example, with the identification of the gene *Antennapedia* in insects (*Drosophila*) and its orthologue, the HOX-gene family, in vertebrates, comparative morphologists and developmental geneticists rushed to generate diagrams of nested sets of clades on which ancestors with hypothesized regulatory gene activity producing different types of appendages could be represented. Continued identification of regulatory genes and gene products seemed to add refinement to scenarios regarding the emergence of morphological novelty, in terms of the structure or form itself as well as in terms of when in phylogeny these structures first appeared.

Today, the belief persists that one can understand the emergence of structural and organismal shape from increasingly more detailed comparisons of entire genomes of different individuals of the same species and different but presumably very closely related species. This, we suggest, is a false impression that is reminiscent of the lack and even dismissal by early 20th century population geneticists of developmental understanding, viz., that it was sufficient to infer genetic factors at the beginning of development from the phenotypes of the adult. Yet we are reminded of Gavin de Beer's

criticism of this notion in *Embryology and Evolution* (1930). To paraphrase de Beer, while population genetics focuses on only two cell divisions, what is more important is the sequence of events that leads to the final form. We believe that de Beer's sentiment is in general still valid. Just because one can identify genes or molecular sequences because of advances in technology, this can no longer be embraced as sufficient to understand the emergence of three-dimensional structure. This myopia also overlooks entirely myriad aspects of, and constraints imposed by, the physical world that not only can have affect, but can also profoundly impact development.

In this regard, we can turn, for example, to D'Arcy Thompson's suggestion in *On Growth and Form* (1917) that not only cell symmetry versus asymmetry but also physical forces such as gravity might play crucial roles in shaping structure. To Conrad Waddington's hint in *Organisers and Genes* (1940) and then to Søren Løvtrup's recognition in *Epigenetics: A Treatise on Theoretical Biology* (1974) that breaking cell-symmetry coincident with gastrulation can lead to a diversity of three-dimensional adult shapes. To George Oster and Pere Alberch's 1982 argument in the journal *Evolution* that differential effects of hydration on cells in conjunction with cell shape can profoundly alter developmental topographies and ultimately structure. And to various contributions, including those of the editors Gerd Müller and Stuart Newman, in *Origination of Organismal Form: Beyond the Gene in Developmental and Evolutionary Biology* (2003), in which physical factors such as cell packing, adhesive interactions, and self-organization are centrally situated in theories of development.

It is in the spirit of these precedent-setting works that we convened this international workshop on the "Biological and Physical Constraints on the Evolution of Form in Plants and Animals." But even more so, we envision this workshop as the one that could have happened in the 1940s but, as the vertebrate paleontologist G. L. Jepsen (1963) bemoaned, never did. Indeed, a gathering of international scholars that, through presentation and discussion, might ultimately collaborate on theoretical issues that reflect not only evolutionary matters specific to plants or animals, but also the spheres of development (and thus evolution) that are *common* to plants and animals. In a first, perhaps tentative step, we hope with this workshop to go beyond the singularly animal-focused "Modern Evolutionary Synthesis" that came to dominate evolutionary biology for more than six decades and consequently overwhelm the few attempts to be taxically if

not theoretically encompassing [see J. Huxley (1940), *The New Systematics*]. We hope our collective efforts will be one of many that will contribute to a true renaissance in evolutionary biology.

Biological and Physical Constraints on Evolution of Form in Plants and Animals

Thu 23 Sept. Evening

6:00 pm WELCOME DINNER (meet in hotel lobby at 5:15 pm)

Fri Sept. 24 Morning General Considerations Chair
Boisvert

9:30 am – 9:40 am Announcements

9:40 am – 10:30 am Müller Organismal Form in Evolutionary Theory

10:30 am – 11:00 am COFFEE

11:00 am – 11:50 am Vergara-Silva Abduction, Deduction, and Induction in
EvoDevo

11:50 am – 12:40 pm Habib Emergence of Convergent Forms Under
Fluid Load in Plants and Animals

12:40 pm – 2:00 pm LUNCH at the KLI

Fri 24 Sept. Afternoon The Physical and Biological Chair
Diggle

2:00 pm – 2:50 pm Newman Physical Determinants in the Emergence
and Inheritance of Multicellular Form

2:50 pm – 3:40 pm Farge Mechano-sensing in Embryonic,
Biochemical, and Morphologic Design and
Evolutionary Perspectives in Primary
Organisms Emergence

3:40 pm – 4:10 pm	COFFEE		
4:10 pm – 5:00 pm	Maresca	Breaking of Symmetry and Development	
6:00 pm	Departure of bus for DINNER		
Sat 25 Sept.	Morning	Development and Physical Constraints	Chair Vergara-Silva
9:30 am – 9:40 am	Announcements		
9:40 am – 10:30 am	Leroi	The Matter With Growth and Form	
10:30 am – 11:00 am	COFFEE		
11:00 am – 11:50 am	Martindale	Changes in the Spatial Position of Gastrulation During Embryogenesis Drive the Rapid Evolutionary Diversification of Bilaterian Body Plans	
11:50 am – 12:40 pm	Miura	Mechanism of Lung Branching Morphogenesis	
12:40 pm – 2:00 pm	LUNCH	at the KLI	
Sat 25 Sept.	Afternoon	Pattern and Regulation	Chair Sanchez-Villagra
2:00 pm – 2:50 pm	Jernvall and Salazar-Ciudad	Staring into the Causality Horizon of the Phenotype	
2:50 pm – 3:40 pm	Diggle	Metameric Development and the Emergence of Plant Form	

3:40 pm – 4:10 pm	COFFEE	
4:10 pm – 5:00 pm	Duboule and Woltering	The Origin of Digits: Patterns vs. Regulations
6:00 pm	Departure of bus for DINNER	
Sun 25 Sept. Morning	Ontogeny and Phylogeny Revisited	Chair Habib
9:30 am – 9:40 am	Announcements	
9:40 am – 10:30 am	Boisvert	From Cells to Structures to Evolutionary Novelties: Creating a Continuum
10:30 am – 11:00 am	COFFEE	
11:00 am – 11:50 am	Sánchez-Villagra	The Evolution of Form: The Contribution of Palaeontology to Our Understanding of Developmental Patterns, as Determined by the Principle of the Conditions of Existence
11:50 am – 12:40 pm	Schwartz	Ontogeny and Phylogeny
12:40 pm – 1:10 pm	All	Participants Discussion
1:10 pm – 2:10 pm	LUNCH	at the KLI
2:15 pm	Departure of bus for WACHAU EXCURSION (back at hotel around 11 pm)	

CATHERINE ANNE BOISVERT

Australian Regenerative Medicine Institute, Monash University, Melbourne,
Australia

**From Cells to Structures to Evolutionary Novelty:
Creating a Continuum**

There currently is a major disconnect in the focus of study for developmental geneticists and evolutionary morphologists; the former being interested in early developmental events at a molecular level in a model animal and the latter in late developmental events or comparison between adult forms, at a structural level in non-model animals. In order to truly integrate information from both fields in our understanding of evolutionary processes, morphology needs to be reintegrated in the study of gene expression and its timeframe needs to be extended beyond early developmental stages. Gene expression in non-model organisms also needs to be studied in order to gain perspective into primitive patterning at evolutionary nodes. Hypotheses formed by the comparison of expression patterns and morphologies seen in extant species can then be tested against forms found in the fossil record, coming closer to understanding the mechanisms underlying evolution.

PAMELA DIGGLE

Department of Ecology and Evolutionary Biology, University of Colorado
Boulder, CO, USA

Metameric Development and the Emergence of Plant Form

The modular or metameric production of parts/organs is fundamental to the generation of plant form. Plant biologists have long considered these repeated units, for example, leaves borne along a shoot, to be inherently similar. I will argue that this assumption, that plant metamers are uniform, is unfounded,

and that examining the sources of variation among metamers is critical to understanding the generation of form and the evolution of morphological diversity. I will review common patterns of positional variation within plant bodies, the distribution of positional variation among lineages, and propose a model for the contribution of positional variation to the evolution of reproductive systems in the genus *Solanum*.

DENIS DUBOULE and JOOST WOLTERING

National Research Centre 'Frontiers in Genetics', University of Geneva, and School of Life Sciences, Federal Institute of Technology (EPFL), Lausanne, Switzerland

The Origin of Digits: Patterns vs. Regulations

The emergence of autopods (hands and feet) as the most distal parts of paired appendages was a key event in the evolution of vertebrates enabling the colonization of terrestrial environments and giving rise to the land vertebrates, the tetrapods. The adaptive potential of various autopodal morphologies (compare an eagle with a horse) has greatly contributed to the success of their subsequent radiation. When, where and how did autopods appear? And how well do we understand the evolutionary relationships between the different digital formulas of various tetrapods? Over the past 25 years the unraveling of the developmental mechanisms behind limb formation, including the discovery of molecular markers, has greatly helped to address these questions. The various weights and meanings given to these molecular markers have however led to controversial views. I will discuss recent proposals regarding the origin of the autopod and digits in particular and point out the necessity to consider regulatory strategies, rather than expression patterns, when using genes to homologize structures in various animals. In the emerging discipline of EvoDevo indeed, the analysis of gene expression patterns can be deceptive without a clear understanding of the underlying regulatory strategies. In this context, I will discuss the adaptive relevance of

evolving stepwise, distinct developmental regulatory mechanisms to build an arm, i.e., a composite structure with functional coherence.

EMMANUEL FARGE

Mechanics and Genetics of Embryonic and Tumoral Development Group,
Institut Curie, Paris, France

Mechano-sensing in Embryonic Biochemical and Morphologic Design and Evolutionary Perspectives in Primary Organisms Emergence

Single cultured cells reactions to mechanical strains have been studied for a few decades. Is mechano-transduction exploited into multi-cellular tissues, and how, is an emergent question of integrative biology. There is increasing number of proofs of the involvement of mechanical cues in inducing both the differentiation and active morphological design of tissues, especially in development. Here we will describe our step-by-step demonstration of the me-mechanical induction concepts in developmental biology, including tumor development. We will speculate that biochemically and morphologically patterned primary ancient multi-cellular organisms might have emerged from such primitive motor-sensorial and differentiation mechano-transduction process.

MICHAEL HABIB

Department of Biology, Chatham University, Pittsburgh, PA, USA

Emergence of Convergent Forms under Fluid Load in Plants and Animals

Very few biomechanists examine both plants and animals in parallel, apparently under a tacit assumption that the rules of shape determination must differ substantially between such distantly related groups. However, convergent structures suggest that the rules of shape governing these groups are largely the same. Such similarities suggest that environmental constraints are important in determining shape, and/or that genomes are more plastic and

prone to morphological convergence than often accepted. I suggest that reference to physical first principles should be made whenever shape is examined in multicellular organisms, regardless of their phylogenetic position. As a case example, I report on the presence of highly convergent structures related to resistance and passive yield under aerodynamic fluid load in plants and animals. I utilize examples from both living and fossil forms, including broad-leaved trees, neornithine birds, and azhdarchid pterosaurs.

JUKKA JERNVAL and ISAAC SALAZAR-CIUDAD

Institute of Biotechnology, University of Helsinki, Finland,
and Facultat de Biociències, Universitat Autònoma de Barcelona, Spain

Staring into the Causality Horizon of the Phenotype

One of the lessons learned from a growing number of developmental biology studies is the multitude of ways that a similar morphological outcome can be obtained. A good example is the mammalian dentition in which different signaling molecules can produce similar changes in the morphology. Yet, the principal aim of most current studies is to discover the lowest level of organization that a specific evolutionary change can be attributed to. We will review current evidence on which levels of developmental regulation (coding and noncoding regulatory sequences, gene interactions, gene networks and epigenetic networks) best explain morphological variation between individuals, populations, species, and higher taxonomic categories. We discuss the most relevant level of regulation as a conceptual barrier, or a causality horizon, that limits the predictability of morphological variation and sets a common yardstick for studies of the genetic bases of morphological evolution. Below the causality horizon, a similar change in morphology is produced differently among taxa. Whereas causality horizon appears to be at the level of individual gene regulation for most available studies comparing populations, there are reasons to believe that it may rise with increasing number of studies, morphological complexity, and taxonomic distance. Future work, especially on

population and species levels, will help to delineate the causality horizon of the genetic basis of morphological evolution.

ARMAND M. LEROI

Department of Biological Science, Imperial College, London, UK

The Matter With Growth and Form

Developmental Biology has largely explained the growth and form of living things in terms of the operation of genetic circuits, that is, the flow of information within and among cells. EvoDevo is accordingly couched in similar terms. But, as Aristotle pointed out more than two millennia ago, the explanation of organic diversity requires not only an account of “form” but also “matter”. That is, a complete explanation of development and diversity also requires an account of where the stuff that creatures use to build their bodies comes from, how it is transformed, and how it is allocated to its various tasks. Here I discuss this problem in terms of the ontogenetic dynamics of metabolism in animals, in particular, the nematode *C. elegans*. I then consider the evidence that growing animals have a unique metabolic programme. Finally, I ask whether the metabolic programs of animals can constrain the diversity of forms of living things.

BRUNO MARESCA

Division of BioMedicine, University of Salerno, Italy

Breaking of symmetry and development

Molecular biology has allowed the identification of genes whose products are responsible for differentiation and embryogenesis (e.g. homeobox genes). However, it is far from being understood how a particular DNA sequence and

its corresponding protein determine cell migration and movement, differentiation, and how symmetries emerge in the embryo. Possibly, the general rules of geometry may generate only a limited number of symmetries in living organisms that may have constrained development and evolution. For ca 3.5 billion years organisms have been unicellular. During the Cambrian explosion a profound reorganization of DNA and its mode of expression occurred, causing the "sudden" origin of Metazoa. This was due also to the appearance of novel genes that were regulated in "time" and "space." Biological complexity evolves in part through processes of diversification during which symmetries are broken and new symmetries appear. Can the general rules of geometry responsible for the appearance of new symmetries constrain the appearance of new forms?

MARK Q. MARTINDALE

Kewalo Marine Laboratory, Pacific Biosciences Research Center, Honolulu, HI, USA

Changes in the Spatial Position of Gastrulation During Embryogenesis Drive the Rapid Evolutionary Diversification of Bilaterian Body Plans

Despite the existence of complex genomes (in terms of gene number as well as family diversity), the body plans of "prebilaterians" appear less sophisticated in terms of tissue complexity and cell type diversity compared to their bilaterian counterparts. Cnidarians (sea anemones, corals, and "jellyfish") are the sister group to the Bilateria, and have been characterized as being radially symmetrical around their oral-aboral axis, and 'diploblastic,' having derivatives of ectodermal and endodermal embryonic tissues with no mesodermal derivatives characteristic of the triploblastic bilaterians. While studying the molecular basis of gastrulation (the formation of ectoderm and the bifunctional endomesoderm) in the starlet sea anemone *Nematostella vectensis* we stumbled upon features of the spatial regulation of downstream components of the Wnt signaling pathway that we argue are key steps into paving the way

for the evolution of the morphological diversity of triploblastic metazoan body plans.

TAKASHI MIURA

Department of Anatomy and Developmental Biology, Kyoto University
Graduate School of Medicine, Japan

Mechanism of Lung Branching Morphogenesis

The vertebrate lung consists of a branched airway tree. The tree structure is generated by repeated splitting of the epithelial tip during development. Numerous molecules are involved in this pattern formation process, but how the interaction of these molecules results in branching morphogenesis remains to be elucidated. We utilize a simple organ culture system and mathematical modeling to elucidate the mechanism of branching morphogenesis in vitro. The principle of the model is the “protrusion grows faster” tendency induced by the depletion of FGF.

The mechanism of branching morphogenesis in vivo is considerably difficult to model because the number of factors involved increases dramatically. To extrapolate the in vitro result to in vivo situation, we utilize the avian lung system and a new primary culture system. We will present the current status of the attempts to understand the mechanism of lung branching morphogenesis in vivo.

GERD B. MÜLLER

Theoretical Biology, University of Vienna, Austria

Organismal Form in Evolutionary Theory

Does the explanation of organismal form require a change in the structure of evolutionary theory? I will argue that it does for at least three reasons: First, the received theory is designed to explain variation at the population level—not the origins of phenotypic structure. Second, its core methodology seeks to provide statistical correlations between phenotypic and assumed genotypic change—not an explanation in mechanistic terms. And third, it relegates all evolutionary solutions of biological form to selectional factors external to the organism—without accounting for any contribution of the generative systems. These immanent restrictions of the so-called Modern Synthesis are overcome by several recent research endeavors that concentrate on the origins of phenotypic complexity. They include, among others, and in addition to different forms of gene regulation, the role of organism-environment interactions, the physical properties of biological materials, and the non-programmed components of cell and tissue formation. The conceptual consequences of these efforts regarding the evolution of form are integrated by EvoDevo theory. Its concentration on generative principles enables an understanding not only of what is adaptively varied but also of what is possible to arise in phenotypic evolution. EvoDevo substitutes the correlational and population focused approach of the Modern Synthesis by a causal-mechanistic explanation and induces significant alterations in the formal structure of evolutionary theory.

STUART A. NEWMAN

Department of Cell Biology and Anatomy, New York Medical College,
Valhalla, NY, USA

Physical Determinants in the Emergence and Inheritance of Multicellular Form

Developmental and evolutionary biology each depend on an understanding of the mechanisms by which morphological phenotypes are produced and inherited. Both fields were advanced over the past century by the recognition that genetic variation was often associated with variations in phenotype. But the genes whose products regulate multicellular development in animals were largely present in unicellular ancestors, and changes in their protein coding or

regulatory sequences during the metazoan radiation cannot by themselves account for the emergence and diversification of animal form. I suggest that novel tissue forms arose when new physical effects and processes were set into motion as certain molecules and pathways of the developmental-genetic “toolkit” came to operate on the multicellular scale. These phenomena include viscoelasticity, surface and interfacial tension, molecular diffusion and reaction-diffusion coupling and other self-organizing effects. The expansion of the set of relevant causal determinants of morphogenesis to include meso-scale physical effects allows us to formulate a set of rules for the inter-generational transmission of form. The grammar of this “pattern language” is simultaneously genetic and physical, providing a common framework for investigating the origination of morphological motifs, the relation of internal and external factors in the shaping of morphological phenotypes, the inter-generation transmission of the conditions of development, and the transformation, stabilization, and integration of organismal form over the course of evolution.

MARCELO R. SÁNCHEZ-VILLAGRA

Paläontologisches Institut und Museum der Universität Zürich, Switzerland

The Evolution of Form: The Contribution of Palaeontology to Our Understanding of Developmental Patterns, as Determined by the Principle of the Conditions of Existence

Evolution happens in deep time, so if we wish to understand the evolution of form, it would be paramount to examine the contributions that fossils can make to this task. A review of published literature, summarized in a web-database, shows that palaeontological data can address mostly late aspects of ontogeny, with palaeohistology its fastest growing field. Indirect information from fossils, even with a uniformitarian approach, reveals developmental novelties. Examples include mechanisms of skeletal mineralization, somitogenesis, and Hox-gene expression domains, and patterns of fish squamation.

Allometric patterns of growth evolve largely coupled with ecological demands, as in the morphological radiation of rodents.

A conceptual framework based on Cuvier's 'conditions of existence' is better suited to understand the evolution of form when studying both living and extinct taxa than the teleology-driven one based on just natural selection or the orthogenetic ideas that dominated palaeontology in the first half of the 20th century.

JEFFREY H. SCHWARTZ

Departments of Anthropology and History and Philosophy of Science,
University of Pittsburgh, PA, USA

Ontogeny and Phylogeny

The first application of von Baer's Laws in an evolutionary context was T. H. Huxley's (1863) case for human relationships lying well within the Order Primates. In spite of the logic of his approach—distinguishing between different levels of taxic inclusivity vis-à-vis commonality in the development and characteristics of emergent features—Haeckel's Biogenetic Law, in which ontogeny reflects a phylogenetic sequence of *adult* ancestors, has largely informed zoo-paleontological (and even neontological) practice. We must situate developmental/ontogenetic information not only in conceiving evolutionary models of species formation (tempo/mode) but also in the methodology of phylogenetic reconstruction with the understanding that while methodologically rigorous because of its hypothetico-deductive underpinnings, a cladistic approach to determining relationships via a hierarchical analysis of character state polarity conflates two different developmental phenomena: the emergence of novel features and their subsequent modification.

FRANCISCO VERGARA-SILVA

Instituto de Biología, Universidad Nacional Autónoma de México, Mexico City,
Mexico

Abduction, Deduction, and Induction in EvoDevo

Recent work on the epistemology of EvoDevo has established that the explanatory goals of this structuralist biological subdiscipline, Form, i.e., characters / developmental types / homolog(ie)s / modules, contrast with the explanatory goals of functionalist, population genetics-based evolutionary biology. Independently, epistemological analyses of phylogenetics (i.e., systematics) have defined the differential participation of the three canonical inferential procedures, abduction, deduction, and (non-probabilistic) induction, both in shaping the theoretical structure of this separate biological subdiscipline and in the justification of its empirical results. Here I use insights from the latter studies to inquire into how inferences are made in EvoDevo, bearing in mind the specificities of its explanatory goals. To ground my epistemological analysis with an example, I refer to published results in plant EvoDevo related to hypotheses on the evolution of the angiosperm flower, which are testable through comparisons of developmental-genetic data from morphologically diverse taxa. Besides advising in project design and the interpretation of empirical (plant) EvoDevo data, I claim that my conclusions might be useful to understand how mathematical/formal modeling and probabilistic inductive inference should be applied in EvoDevo studies.