ALTENBERG SEMINARS IN THEORETICAL BIOLOGY

Winter 2008/2009:
Modularity

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

Program:

13 November 2008
Chris KLINGENBERG
(Faculty of Life Sciences, University of Manchester):
Developmental Integration and Modularity: Inferences from Morphology

27 November 2008
Thomas F. HANSEN
(Centre for Ecological and Evolutionary Synthesis, University of Oslo):
Measuring Evolvability and Constraints in Complex Characters

8 January 2009
Jessica BOLKER
(Department of Biological Sciences, University of New Hampshire):
Modularity: Putting the Pieces Together

22 January 2009
Claudia Lorena GARCIA
(Institute of Philosophical Research, National Autonomous University of Mexico):
Functional Modularity and the Structure of Mind

The topic

Hierarchy "is a property of nature, not only a conceptual scheme for organization" (VRBA & GOULD 1986: 217). Most of the complex systems we encounter in the world—from atoms to galaxy clusters—have clearly hierarchical structures: they consist of subsystems, which consist of subsystems, etc. The components interact with each other, but the frequencies associated with their interactions drop steadily as one moves upward in the hierarchy—typically by an order of magnitude or two for each level one ascends (SIMON 1962). A module is to be understood most generally as a component of a larger system that operates largely independently of other components. More specifically, modules are characterized by the integration of their (sub)components and by their autonomy vis-à-vis aspects of their environment. (See SCHLOSSER & WAGNER 2004 and CALLEBAUT & RASSKIN-GUTMAN 2005 for more specific definitions and a variety of applications.) It is the ubiquitous modularity of most natural (as well as artificial) systems that largely explains why they are "nearly decomposable" (SIMON), which in turn makes plausible that a reliable understanding of complex systems is attainable by us cognitively "bounded" beings at all (see, e.g., BLUME & APPEL 1999).
Although hierarchy is a central phenomenon of life as well as of inorganic nature, it did not feature prominently in biological theory until quite recently. Yet, a general theory of biology ought to be "a theory of hierarchical levels—how they arise and interact" (VRBA & ELDREDGE 1984: 146; cf. BOLKER seminar). A hierarchical living world contains entities such as genes, organisms, species, etc. that act as "evolutionary individuals" at several levels of ascending inclusion. In such a world, the traditional equation of selection—a causal process—and sorting—differential birth and death among varying organisms within a population—no longer holds: Sorting can arise from selection at the focal level itself, and as a consequence either of downward causation from processes acting on individuals at higher levels or upward causation from lower levels (VRBA & GOULD 1986). Likewise, during development, components that operate as integrated and context-insensitive units ("developmental modules") have been recognized at many different levels ranging from molecular interactions to entire organisms (see, e.g., CARROLL et al. 2001).
The recent surge in interest in modularity among biologists stems mostly from accumulating evidence that some of the modular units of development were highly preserved but "promiscuously recombined" during evolution, fueling hopes that understanding developmental and/or behavioral modularity will provide deep insights into constraints on evolution (SCHLOSSER & WAGNER 2004). But the underlying assumption that modules of development will act as coherent and "quasi-independent" (Richard LEWONTIN) units of evolutionary transformations, as it turns out, is not necessarily true. In order to make an independent fitness contribution (i.e., to accomplish "autonomy" in the afore-mentioned sense), developmental modules must not only be quite invariant vis-à-vis the environment in which they are imbedded (regardless of whether they themselves have strong effects on their surroundings or not) but also be relatively isolated regarding their functional effects—say, locomotion or sensory functions). Different developmental modules with an overlapping genetic basis may be linked together into a single module of evolution by frequent pleiotropic effects of heritable variations (WAGNER & ALTENBERG 1996). One important open question is whether modules arise through the action of natural selection or because of biased mutational mechanisms (WAGNER et al. 2004).
In the opening seminar, Chris KLINGENBERG will illustrate the use of morphometric methods and model systems to investigate how development produces covariation between traits, and how this affects evolution. Jessica BOLKER will focus on the status of modules (in particular species) as individuals, how they interact, and the ways in which they arise, transform, and function through time. The question under what precise conditions modularity can be expected to enhance evolvability will be at the center of both Thomas HANSEN's and Claudia Lorena GARCÍA's seminars. Whereas the first three seminars will consider modularity primarily from the perspective of evolutionary developmental biology (EvoDevo), GARCÍA will expand EvoDevo-type considerations to discuss, and criticize, aspects of the influential "massive modularity" thesis in recent philosophy of mind.

References

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CARROLL SB, GRENIER JK, WEATHERBEE SD (2001) From DNA to Diversity. Blackwell Science.

SCHLOSSER G, WAGNER GP, eds (2004) Modularity in Development and Evolution. U. of Chicago P.

SIMON HA (1962) The architecture of complexity. Proceedings of the American Philosophical Society 106: 467-482.

VRBA ES, ELDREDGE N (1984) Individuals, hierarchies and processes: Towards a more complete evolutionary theory. Paleobiology 10: 146-171.

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WAGNER GP, PAVLICEV M, CHEVERUD JM (2004) The road to modularity. Nature Reviews Genetics 8: 921-929.

Abstracts and biographical notes

Chris KLINGENBERG
Faculty of Life Sciences
University of Manchester

Developmental Integration and Modularity: Inferences from Morphology

Thursday 13 November 2008

Abstract

Biological systems, from molecular complexes to whole organisms and ecological interactions, tend to have a modular organization. Modules are sets of traits that are internally integrated by interactions among traits, but are relatively independent from other modules. From the morphologist's perspective, developmental interactions are of particular interest, because they influence structural, functional, and genetic patterns of integration, and therefore have a potential influence on evolutionary processes and patterns. I use morphometric methods and several model systems to investigate how development produces covariation between traits, and how this affects large-scale evolutionary patterns.

Biographical note

Christian KLINGENBERG has been a senior lecturer in the Faculty of Sciences, University of Manchester since 2003. He studied biology at the universities of Berne, Switzerland and Kiel, Germany (lic. Phil.-nat., 1988), and completed his PhD degree in Systematics and Evolution at the University of Alberta, Canada. He was a postdoctoral fellow in Fred NIJHOUT's group in the Department of Zoology at Duke University (1997-99) and in Michael AKAM's group in the Laboratory for Development and Evolution, University Museum of Zoology, Cambridge, UK. Before moving to Manchester Dr. KLINGENBERG was an assistant professor in the Department of Biology at the University of Konstanz.

Selected publications

(2008) Novelty and "homology-free" morphometrics: What's in a name? Evolutionary Biology 35: 186-190.

(2008) The pace of morphological change: Historical transformation of skull shape in St Bernard dogs (with A. G. DRAKE). Proceedings of the Royal Society of London B 275: 71-76.

(2008) Morphological integration and developmental modularity. Annual Review of Ecology, Evolution and Systematics 39: 115-132.

(2007) Integration of wings and their eyespots in the speckled wood butterfly Pararge aegeria (with C. J. BREUKER, M. GIBBS, H. VAN DYCK, P. M. BRAKEFIELD, & S. VAN DONGEN) . Journal of Experimental Zoology (Molecular and Developmental Evolution) 308B: 454-463.

(2007) Developmental buffering: How many genes? (with J. S. PATTERSON). Evolution and Development 9: 525-526.

(2006) Functional evo-devo (with C. J. BREUKER & V. DEBAT). Trends in Ecology and Evolution 21: 488-492.

(2006) A single basis for developmental buffering of Drosophila wing shape (with C. J. BREUKER & J. S. PATTERSON). PLoS ONE 1(1): e7.

(2006) Hsp90 and the quantitative variation of wing shape in Drosophila melanogaster (with V. DEBAT, C. C. MILTON, S. RUTHERFORD, & A. A. HOFFMANN). Evolution 60: 2529-2538.

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(2005) The genetics and evolution of fluctuating asymmetry (with L. J. LEAMY). Annual Review of Ecology, Evolution and Systematics 36: 1-21.

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(2004) Integration and modularity of quantitative trait locus effects on geometric shape in the mouse mandible (with L. J. LEAMY & J. M. CHEVERUD). Genetics 166: 1909-1921.

(2003) Quantitative genetics of geometric shape: Heritability and the pitfalls of the univariate approach. Evolution 57: 191-195.

(2003) Developmental integration in a complex morphological structure: How distinct are the modules in the mouse mandible? (with K. MEBUS & J. C. AUFFRAY). Evolution and Development 5: 522-531.

(2002) Morphometrics and the role of the phenotype in studies of the evolution of developmental mechanisms. Gene 287: 3-10.

(2001) Inferring developmental modularity from morphological integration: Analysis of individual variation and asymmetry in bumblebee wings (with A. V. BADYAEV, S. M. SOWRY, N. J. BECKWITH). American Naturalist 157: 11-23.

(2001) Genetic architecture of mandible shape in mice: Effects of quantitative trait loci analyzed by geometric morphometrics (with L. J. LEAMY, E. J. ROUTMAN, & J. M. CHEVERUD). Genetics 157: 785-778.

Thomas F. HANSEN
Centre for Ecological and Evolutionary Synthesis
Department of Biology, University of Oslo

Measuring Evolvability and Constraints in Complex Characters

Thursday 27 November 2008

Abstract

A fundamental question in evolutionary biology is whether adaptation is constrained by a lack of evolutionary potential. We know that most traits harbor high levels of mutational variance and additive genetic variance, and should be evolvable. It is, however, not clear to what extent this variation is free of pleiotropic constraints from other characters. To investigate this question, we need precise ways to measure the evolvability, constraint, and integration of complex multivariate characters. I will present some suggestions for how to do this, and show some applications.

Biographical note

Thomas HANSEN has been Professor in the Centre for Evolutionary and Ecological Synthesis, Department of Biology, University of Oslo since 2006. He studied at the University of Oslo (BA, 1988; MA in Zoology, 1990; PhD on "Adaptation, Phylogeny, and the Comparative Method," 1997). He previously worked in Mike LYNCH's and Emília MARTINS's labs at the University of Oregon, in Günter WAGNER's lab at Yale, and in W. Scott ARMBRUSTER's lab at the University of Trondheim. From 2000 to 2005 he was assistant professor in the Department of Biological Sciences at Florida State University.

Selected publications

(2007) A theoretical investigation of sympatric evolution of temporal reproductive isolation as illustrated by marine broadcast spawners (with M. TOMAIUOLO & D. R. LEVITAN). Evolution 61: 2584-2595.

(2006) The evolution of genetic architecture. AREES 37: 123-157.

(2006) Evolution of genetic architecture under directional selection (with J. M. ÅLVAREZ-CASTRO, A. J. R. CARTER, J. HERMISSON, & G. P. WAGNER). Evolution 60: 1523-1536.

(2006) On adaptive accuracy and precision in natural populations (with A. J. R. CARTER & C. PÉLABON). American Naturalist 168: 168-181.

(2006) The origins of robustness. Evolution 60: 418-420.

(2005) The role of epistatic gene interactions in the response to selection and the evolution of evolvability (with A. J. R. CARTER & J. HERMISSON). Theoretical Population Biology 68: 179-196.

(2005) Assessing current adaptation and phylogenetic inertia as explanations of trait evolution: The need for controlled comparisons (with S. H. ORZACK). Evolution 59: 2063-2072.

(2004) Floral integration, modularity, and precision: Distinguishing complex adaptations from genetic constraints (with W. S. ARMBRUSTER, C. PÉLABON, & C. P. H. MULDER). In: Phenotypic Integration (PIGLIUCCI M, PRESTON K, eds), 23-49. Oxford UP.

(2004) Evolvability, stabilizing selection, and the problem of stasis (with D. HOULE). In: Phenotypic Integration (PIGLIUCCI M, PRESTON K, eds), 130-150. Oxford UP.

(2003) Epistasis in polygenic traits and the evolution of genetic architecture under stabilizing selection (with J. HERMISSON & G. P. WAGNER). American Naturalist 161: 708-734.

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(2003) Evolution and detection of genetic robustness (with J. A. G. M. DE VISSER, J. HERMISSON, G. P. WAGNER, L. W. ANCEL, H. BAGHERI, J. L. BLANCHARD, L. CHAO, J. M. CHEVERUD, S. M. ELENA, W. FONTANA, G. GIBSON, D. KRAKAUER, R. C. LEWONTIN, C. OFRIA, S. H. RICE, G. VON DASSOW, A. WAGNER, & M. C. WHITLOCK). Evolution: 57: 1959-1972.

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(1997) Stabilizing selection and the comparative analysis of adaptation. Evolution 51: 1341-1351.

(1997) Phylogenies and the comparative method: A general approach to incorporating phylogenetic information into the analysis of interspecific data (with E. P. MARTINS). American Naturalist 149: 646-667.

(1996) Translating between microevolutionary process and macroevolutionary patterns: The correlation structure of interspecific data (with E. P. MARTINS). Evolution 50: 1404-1417.

Jessica BOLKER
Department of Biological Sciences
University of New Hampshire

Modularity: Putting the Pieces Together

Thursday 8 January 2009

Abstract

The concept of modularity is used, and independently defined, in disciplines ranging from business to biology. Even within biology, different fields use the term in different ways. I will explore the extent to which various usages are (or are not) commensurable, and the implications for our ability to use modularity to bridge fields and levels of biological organization—in particular, to connect development and evolution.
Core questions about biological modules center on their status as individuals, the nature of their interactions, and the ways in which they arise, transform, and function through time. These questions closely mirror long-running debates within evolutionary biology about species, a central and well-examined type of evolutionary module. I will examine whether approaches to defining and understanding the dynamics and function of species may be applied to modularity more generally.
The language of modularity offers a powerful way to describe and interpret patterns of biological organization at many levels. When we propose particular entities as biological modules, we posit a conceptual model of how a specific biological system is organized. As with any model, whether conceptual, biological, or computational, it is important to examine the relationship between our concepts of modularity, and the biological reality we intend them to represent.

Biographical note

Jessica BOLKER is Associate Professor in the Department of Biological Sciences at the University of New Hampshire, and Associate Director of the Shoals Marine Laboratory. She studied biology at Yale University (BS, 1986), and spent a year as a visiting scholar at St. John's College, Oxford before earning a PhD in Zoology at the University of California at Berkeley in 1993. She was a postdoctoral researcher at Indiana University, Bloomington from 1994-97, and joined the Zoology Department at the University of New Hampshire in 1998. She has studied the embryology of sturgeons and sea urchins, pigmentation development in flounders, and the evolution of morphogenetic mechanisms. Her theoretical and philosophical interests span a range of issues including modularity, homology, the role of fictional species in real science, the interfaces among development, ecology, and evolution, and epistemological questions related to the use of model systems.

Selected publications

(Submitted 2008) Exemplary and surrogate models: Two modes of representation in biology. Perspectives in Biology and Medicine.

(2005) Defining a meeting place: Modularity in development and evolution. Evolution 59: 1383-1386.

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Claudia Lorena GARCIA
Institute of Philosophical Research
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Functional Modularity and the Structure of Mind

Thursday 22 January 2009

Abstract

A controversy concerning the cognitive architecture of the human mind has preoccupied cognitive scientists for a long time. One of the relatively recent parties to this controversy groups together some cognitive evolutionary psychologists, cognitive anthropologists, philosophers, and neuropsychologists. They argue that the mind is mostly constituted of cognitive modules—information processing mechanisms that admit only certain kinds of information as input and that are functionally specialized, operationally autonomous, and informationally encapsulated. Recently, some of these "massive modularists" have offered an additional argument in favor of the massive modularity of the mind: They argue that, since the architecture of the mind is the product of evolution by natural selection, and since structures and systems that are functionally modular are more evolvable than those that are not or less so, it is probable that the mind is mostly made up of functional modules. Here I show that at present there is no evidence of any sort, either empirical or otherwise, to think that functional modularity in any way enhances evolvability; that, furthermore, there is some indirect evidence suggesting that functional modularity is either orthogonal or even (in one case) opposite to evolvability.
Now, functional modularity in the cognitive sciences—and in particular in the appropriate literature concerning massive modularity—is usually understood in terms of functional specialization. On the other hand, in EvoDevo, where the discussion concers the properties of systems that may or may not enhance their evolvability, functional modularity tends to be understood instead in terms of either functional integration or functional independence. I present some of the concepts of function that are in use both in evolutionary biology and the cognitive sciences. Then I analyze the aforementioned notions of functional modularity, show that they are each distinct from the others, and explore the connections they may either have or lack with different concepts of function that are presented in the previous section. Finally I show that (1) there is no conceptual and/or empirical evidence to think that a trait's being functionally modular to a large degree increases the probability of its being more evolvable than traits that are not, or less, functionally modular; and (2) there is some indirect empirical evidence from evolutionary biology strongly suggesting that functional integration goes indeed in the direction contrary to evolvability, and that both functional specialization and independence are simply unrelated to evolvability.

Biographical note

Claudia Lorena GARCÍA AGUILAR has been a researcher at the Instituto de Investigaciones Filosóficas, Universidad Nacional Autónoma de México, since 1994. She studied philosophy at UNAM (BA, 1981) and at the University of Southern California (MA, 1983; PhD, 1989). Dr. GARCÍA has previously been assistant professor in the philosophy departments at Northern Illinois University (1989-91) and Texas Tech (1991-94), visiting professor in the Department of Philosophy, University of Wisconsin, Madison (1990), and visiting scholar at the University of California, San Diego (2000-01).

Selected publications

(2007) Cognitive modularity, biological modularity, and evolvability. Biological Theory 2: 62-73.

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