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Complex Organismal Functions: Integration and Evolution in Vertebrates
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Introduction

Diversity and complexity characterize life. The student of living organisms is overwhelmed by the multitude of forms and functions, of modes of survival, of life histories and reproductive strategies, and of behavioral and ecological adaptations. This diversity of life stands in sharp contrast to the apparent uniformity of processes in the inanimate world and is taken by many to represent an "emergent property" of living systems. While classical physics-oriented science is characterized by the successful search for unifying principles and laws, life is viewed as an opportunistic process which has evolved along many diverse pathways.

The complexity of organisms certainly transcends that of inanimate, individual systems, whether static or dynamic. Progress in many fields of biology has been characterized by a growth in understanding of the complexity of organisms, rather than a reduction to a few underlying principles. Biological complexity is characterized not only by the number and diversity of components of organisms but, most of all, by the interconnections among these components. Biological complexity is seen by many to differ from physico-chemical complexity in principles of individuation and self-organization, hierarchy, "downward causation," and the like, which give the whole organism a certain autonomy with respect to its subsystems. There is a strong element of history in biological complexity, perhaps most clearly evidenced by the great persistence of bauplans and the failure of new bauplans to emerge in hundreds of millions of years. This indicates that fundamental patterns of the organization of life self-stabilize.

While diversity and complexity in biology are difficult to comprehend fully even when considered separately, the analysis becomes even more complicated when we try to bring the phenomena together in the framework of one of the few unifying principles in biology: evolution. Acceptance that diversity and complexity of living organisms both result from past evolutionary events leads to a basic paradox. On the one hand, organisms are tightly coupled systems at genetic, developmental, structural, and functional levels, and this constitutes a high degree of integration that is a fundamental prerequisite for self-production and self-maintenance, unique features of life. Such systems are finely equilibrated, but at the same time extremely sensitive to changes and disturbances at critical points of the interactive, self-maintaining network. On the other, evolution has led to fundamental changes in the organization of organisms. Yet they have had to remain integrated and stabilized throughout the entire process of their evolution. Increase in complexity of systems apparently has led to an increase in self-stabilization, but this seems to counteract markedly the tendency of evolution to increase diversity. Any modifications in such complex systems must be compatible with the functioning of all stages in the life of an organism, for all changes are basically modifications of ancestral ontogenetic trajectories.

Therefore, a fundamental question in biology is: How is evolution as a process that leads to an increase in diversity compatible with evolution as a process that leads to an increase in complexity and self-stabilization? This and related questions led us to propose a Dahlem Workshop to consider how complex, integrated systems evolve within the context of increases in organismal diversity.

In order to provide a coherent set of topics in sufficient detail to permit useful discussion, we limited the workshop to problems in the evolution of vertebrates. By this decision we make no claim that vertebrates are more complex than other groups of animals, or plants, or that they occupy some special position in biology. The problems selected for discussion have a solid empirical foundation for vertebrates, and only for pragmatic reasons were students of such fascinating groups as insects and orchids, for example, not included.

We selected three primary areas for discussion. We reasoned that, at least for the vertebrates, adaptive radiations of lineages appear to be based primarily on modifications of feeding, locomotory, and reproductive systems. Accordingly, the first area selected for discussion deals with the evolution of feeding mechanisms, which we perceived as being generally integrated through the structure and function of the brainstem. The second is the evolution of locomotor systems, with integration being provided primarily by components of the spinal cord. For the third area we wanted to have a topic related to reproduction. In order to provide more focus for the discussions we selected the evolution of a particular mode, viviparity, which we consider to be integrated by a neuroendocrinological axis. A fourth discussion topic might have centered on problems in development and embryology as they related to the evolution of complexity, but it was decided that development should be considered together with structure and function in each of the three major discussion areas. The fourth general topic selected for discussion was focused more explicitly on different approaches to the study of the evolution of complexity in organisms. There is a tension between those who might be called classical neodarwinists and those biologists who believe that neodarwinian perspectives are deficient in dealing with the evolution of organismal complexity. The fourth group was asked to characterize the controversies, to attempt to find areas of common ground, and to identify areas of disagreement. We did not expect that the disagreements could be made to disappear, but we hoped that by making them explicit the combatants could better understand each other and work in the long term toward the goal of a unified conception of organismal evolution.

Comparative anatomists and functional morphologists who deal with the empirical core of the topics for discussion constituted the largest identifiable group of participants. It was important that a wide diversity of views be represented, and accordingly the participants included ecologists, behavioral and neurobiologists, physiological ecologists, endocrinologists, quantitative geneticists, paleontologists, and representatives of other disciplines, including theorists.

The conference was held in the late summer of 1988, and the general view of participants was that it was a stimulating and exciting workshop. While no major problems were solved, substantial progress was made in defining issues and in identifying problems and possible productive avenues of future research. There were substantial disagreements on many points, and yet we found many areas of common ground. Even though there were many hotly debated topics there was a great deal of good will and a willingness to listen to alternative viewpoints and interpretations.

We found that words and their meanings caused considerable difficulty from time to time, and we were encouraged by several participants to prepare a glossary. However, we remembered intense debates concerning the precise meaning of such words as "complexity," "integration," "coupling," "stability," "key innovation," and many others, and it finally seemed best to permit the reader to understand the meaning of these words by context and by reference to the background literature. It would be presumptuous to give our definition to words that mean different things to different authors.

The background papers, discussions, and group reports in combination conclude that the vertebrate organism represents a highly integrated and coupled system, both with regard to different structures and functions at the same hierarchical level, and to cross-level relationships (from molecules and cells to ecology). This integration and coupling is the source of strong resistance to structural and functional changes, which tend to occur in particular patterns and directions. The kinds of couplings that seem to be particularly important include:

1. Genetic coupling: pleiotropy, epistasis, genetic disequilibrium, and genetic correlations, which can produce changes in one structure (or function) as a result of changes in another, quite unrelated structure, or prevent certain kinds of changes from occurring.

2. Ontogenetic coupling: certain structures or functions as necessary preconditions (precursors, organizers, inducers, etc.) for the formation of other structures and functions.
3. Functional coupling of different structures (e.g., coupling of skeletal, muscular, respiratory, cardiovascular, and nervous systems in locomotion).
4. Structural coupling of different functions: the same structures participating in different functions (e.g., feeding, breathing, and calling in anuran amphibians accomplished by branchial structures).

These types of coupling often lead to phenomena of stasis because a functional system coupled structurally to another functional system, or a structural system coupled functionally to another structural system, cannot change easily or optimize without changes in the other; they restrict the evolution of each other. In most cases, internal (associated with functional and development systems in organisms) and external (environmental) selection acts differently on the different subsystems. Accordingly, as many chapters in this volume document, uncoupling in a genetic, ontogenetic, functional, or structural context often is the major precondition for the origin of novelties.

However, the introduction of evolutionary novelties is not necessarily based on "dramatic" uncoupling of previously tightly coupled systems. Articles in this volume give illuminating examples concerning the formation of new complex functional systems that are based on long cascades of events, often seemingly unrelated. Such cascades are found, for example, in the evolution of the mammalian masticatory system that included formation of secondary jaw structures, new patterns of tooth replacement, new muscles, new motor nuclei, and other features. Other examples are the evolution of the mammalian locomotor system, which includes changes in the pelvic girdle, shoulder girdle, coupling of locomotor, respiratory, and cardiovascular system; the evolution of avian flight, which involves endothermy, changes in structure and function of the cardiovascular and respiratory systems, the development of air sacs, and changes in brain structure and function; and the evolution of viviparity, which involves internal fertilization, retention of the egg, communication between the parent and the conceptus, and changes in the neuroendocrine axis.

Externalist and internalist perspectives emerged at many points during discussion, and difficulties in communication often gave the impression of different concepts of how evolution proceeds. To a large measure these differences were exposed as matters of degree of emphasis, but not all conflicts were settled. Those participants with internalist biases emphasize the generation of form and the restrictions on appearance of phenotypic variants, while those with externalist biases focus on the performance of

variant phenotypes and are not so concerned with the details of embryological processes and ontogenetic pathways. While the focal level of discussion was the organism, the value of hierarchical approaches to the study of transformations of organismal form became evident.

Evolutionary biology is being enriched by the incorporation of many more perspectives than in the past. These include internalist views on the centrality of the organism (concepts of coupling, interactions in development, systems of constraints, integration, and the like), phylogenetic perspectives on hierarchy, historical contingency and constraints, and new externalist approaches involving direct application of quantitative genetic methods to natural populations observed through time. All of these perspectives, and more, were manifest in this workshop, which was a vivid example of the opportunities inherent in integrative, multidimensional approaches to the study of the evolution of complex systems.

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