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DISCUSSION GROUP

Development and Evolution— The Emergence of a New Field

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The occasion of the Fourth International Congress of Systematic and Evolutionary Biology, in College Park, Maryland, provided the opportunity for a "Round-table Discussion Group" to explore ideas and opportunities for research on the relationship of development to morphological evolution. What was planned as a tightly organized discussion by a small working group quickly changed when over 200 individuals filled a large, formal lecture hall. A lively discussion ensued, despite the size of the group. The present report is not a summary of that discussion, but an attempt to distill from it the central issues.

OVERVIEW

The most general impression gained by the authors as a result of the four-hour discussion is the widespread acknowledgment within the evolutionary biology community that findings in the area of developmental biology have a central relevance for evolutionary studies. The heralded synthesis that occurred following the integration of genetic principles into evolutionary studies by theorists such as Haldane, Fisher and Wright ultimately failed to incorporate developmental biology (although attempts were made by some, including de Beer and Schmalhausen), almost certainly because development remained too much of a "black box." In recent years, however, the spectacular gains in developmental biology have highlighted: 1) the opportunity to test hypotheses in evolutionary and developmental biology concerning morphological evolution by direct experiments, 2) the opportunity to incorporate a new body of facts and new theories of development into the framework of evolutionary theory, and 3) the need for a phylogenetic and evolutionary perspective in developmental biology. It is the reciprocity between disciplines that interests both evolutionists and developmentalists, and raises the possibility of new kinds of interaction that might substantively benefit both fields. The question is no longer simply "What do facts of development offer to evolutionary biology?",

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but also "What can evolutionary biology offer to students of development?". It is the possibilities for new synergisms, of the heuristic value of interdisciplinary interaction, and of the opportunities of an expanded evolutionary and developmental synthesis that excite the imagination.

There was a general sense in the discussion that the current organization of science, with its sharp subdivisions (often reinforced by the organization of funding agencies), acts as a deterrent to the expansion of what was seen by discussants as a new discipline. This new discipline is emerging at the confluence of three traditional areas of study: development, evolution, and phylogenetics. Within the area of development at least two major foci of major significance for evolution are evident, the first being the genetics of development (with reference to direct and indirect effects on trait differences), and the second being mechanisms of morphogenesis and pattern formation (including the study of cell and tissue interactions and the mechanics of development, among a wide array of investigations). Within the area of evolution the principal focus is quantitative genetics, which is seen as a link between genetic (and developmental) phenomena and evolutionary theory. Emphasis also has been given to the nature and generation of phenotypic variation, in particular discrete alternative morphological states, on which natural selective processes are based. Within the area of phylogenetics the principal foci of investigation are the role of historically acquired functional and developmental constraints, and the evaluation of the frequency and causes of homoplasy (and the attendant message that morphological outcomes are limited), as well as the value of development in understanding character state transformation.

There is as yet no consensus as to whether the intellectual effort of this new field should proceed along strict functionalist (neoDarwinian) lines, with an emphasis on population-level phenomena, along strict structuralist lines, with an emphasis on form-generation, or in an explicitly synthetic framework, in which both perspectives are pursued equally and simultaneously, with priority given to neither. Yet, without doubt, a new field has arisen.

This new area of investigation is synthetic, incorporative and integrative. It may need a label, but not because, as some have said, "when concepts fail, a name will suffice," but because the concepts are beginning to fall into place and the work before us is beginning to take form. One participant has suggested "evolutionary embryology" as the most appropriate identifier for the new field. We need better communication, and we need ways to identify colleagues with similar interests and approaches, perhaps through a dedicated journal. Finally, we need to communicate effectively with administrators and bureaucracies in order to have influence on planning and to assure appropriate levels of funding. Our work is diverse, and broadly distributed across different levels of biological organization, involving diverse taxa. Young people, attempting to find positions in traditional university departmental structures, are most keenly aware of the need for identity.

Despite lively discussion on these matters and many positive suggestions, there was no consensus as to what should be done, but little disagreement that something should be done. Perhaps the success of the general endeavor speaks for itself, for many papers are already published, many students are attracted to the area, and obviously much research is being conducted.

The question before us is whether the area of study should remain interdisciplinary, with all of the diffuse and unorganized features that have characterized it to date, or if a new field should be identified, with some central principles and goals. At least one speaker believes that a central problem impeding a successful synthesis and integration of developmental and evolutionary biology is the absence of a comprehensive theory of development. It may be that those who wish to work in the new field must receive training in the principles and methodologies of cell and molecular biology, the area in which the largely unheralded revolution in development is occurring.

ORGANIZATION OF THE DISCUSSION

The discussion was divided into four segments. Gunter Wagner led a general discussion of the hierarchy of developmental processes and patterns. Three general questions were pursued: 1) What developmental mechanisms are involved in the generation of both morphological order and novelty? 2) Can hierarchical approaches (ontogenetic, phylogenetic, and levels of organization) contribute to our understanding of the relationship between development and morphology in evolution? 3) What is the relationship among genetic, developmental, structural and functional constraints with respect to the evolution of morphology?

A discussion of the developmental origin of evolutionarily significant morphological change was led by James Hanken. Topics considered included: 1) How do developmental systems become decoupled, and how does this decoupling provide opportunities for evolutionary change? 2) How do developmental constraints restrict evolutionary change, and to what degree do they channel (or direct) any morphological change that occurs? 3) What developmental mechanisms underlie heterochrony, and to what degree is heterochrony indicative of the genetic basis of evolutionary change?

Paula Mabee led a general discussion of ontogeny and systematics. Among the questions pursued were: 1) What developmental components of homology can be identified, and can homologous structures have very different ontogenies? 2) How important is heterochrony, and how does it relate to taxic and transformational aspects of morphological evolution? 3) How can ontogenetic information be used in systematics?

The final discussion segment, on prospects for the general area of the relation of development to morphological evolution, was led by David Wake. The questions pursued included: 1) What can evolutionary morphology and systematics offer students of development? 2) What can we expect from new molecular and quantitative genetic approaches applied to development, other than more data? 3) What are the components of a discipline of evolutionary developmental biology?

Discussion was free and wide-ranging, but at the same time both meaningful and provocative. The overview presented here focuses not on the details or formal sequence of the discussion, but on the general principles that emerged.

HETEROCHRONY

Heterochrony immediately arose as a central focus in several of the discussions. Heterochrony (a change in developmental timing, relative to an ancestor) is an evolutionary term that describes the result (a phylogenetic pattern) of a process or combination of processes; it can be known only in a phylogenetic context. Because specific developmental events can be perceived as resulting from shifts in timing of genetic or morphogenetic processes, many workers have discussed heterochrony as if it were a process or even a mechanism, and this has led to both ambiguity and confusion in the literature (evident in such terms as "heterochronic genes"). The term heterochrony is best viewed as a pattern, and a phenomenon that is discernible through comparisons conducted in a phylogenetic context.

Assessments of the importance of heterochrony range from maximal, often ascribing major patterns of lineage evolution to the phenomenon, to minimal or trivial. Some discussants argued that there have been surprisingly few general novelties since the Cambrian (a point commonly made in the literature), in terms of new body plans, tissue types, or morphogenetic rules. For this reason alone, many phylogeneticists think that most major evolutionary events are the result of a phylogenetic reshuffling (in which heterochrony is dominant) of developmental events. Extending this argument, if major events arise from heterochrony, it also is likely that much morphological diversification at lower taxonomic levels is the result of heterochrony. Skeptics counter by claiming that in such arguments heterochrony becomes a universal redescriptor, and that virtually all evolutionary modifications can be couched in this context with no useful outcome. Some see heterochrony as an epiphenomenon at an organizational level above a heterogeneous assemblage of processes at another level. Viewed in a phylogenetic perspective, this is not a problem, but in a more narrow evolutionary mechanism framework it is. However, even when viewed as a result, there is widespread disagreement concerning the importance of heterochrony.

As a general pattern, heterochrony is evident at the level of character evolution, at the level of evolutionary changes in the integration (coupling and decoupling, and the degree to which these occur) of groups of characters, and at the level of the whole organism. The degree to which heterochrony might be useful depends on the research strategy and goals of different investigators.

Classifications are intended to convey information, and the classification schemes that have been used with respect to heterochrony have reached some stability; there appears to be wide agreement on terminology and this has improved communication among biologists investigating the relationship between developmental and evolutionary change. However, workers are beginning to question the usefulness of this terminology. A common accusation is that classification of a pattern often does not contribute to an explanation of its cause. Not all patterns that appear to be, or are construed as, representative of changes in developmental timing, are such. But, because classification systems are necessary for progress (they often motivate and direct research), how can processes of relevance to developmental biologists be most appropriately classified in an evolutionary context? If data are simply amassed without the context of an organizing framework, which a classification can provide, we have no way of determining progress toward some goal, and simply await the emergence of a new paradigm, which may never appear.

Some suggestions were made concerning future classifications of development in relation to evolutionary change. One scheme might classify according to types of developmental mechanisms or known processes. Another might classify according to establishment of systems of coupling and decoupling of developmental processes (such as subsystems within an organism—bone and cartilage in skull formation in a vertebrate, segments within an insect, sequential leaves in an angiosperm). Perhaps we need different classification schemes appropriate to different levels of organization. There is a need for a holistic classification, at the level of whole organisms, that at the same time permits experimental exploration. Some enthusiasm was expressed for the analysis of coupling/decoupling for this reason, because coupling is an evolutionary statement that is simultaneously a statement concerning developmental mechanism. Empirical investigation requires a hypothesis of phylogenetic relationships among investigated taxa, a set of characters that vary in their correlations, characters whose sequence of appearance in ontogeny varies, and an experimental developmental approach for investigating the system. Direct experimental interventions and quantitative genetics might well be incorporated in such a framework of study. In order to interpret the evolution of developmental changes, a phylogenetic context is required.

DEVELOPMENTAL CONSTRAINTS

The notion of constraint is widespread, and has been the subject of much investigation and controversy. The most general argument in its favor is the fact that lineages evolve within evident limits, as perceived by the occupancy of morphospace, but there seem to be few profound constraints (an example is bilaterality in many groups). Developmental constraints are evident principally in biases in the production of phenotypes. That structures can be identified as homologues is in itself an argument for the reality of developmental constraints. A primary reason for the ubiquity of homoplasy in evolution may be constraints on the production of form. The effects of constraints can be general. An example is the upward causation of genome size on cell size, and its apparent large effects on morphogenesis (manifest directly in changes in developmental rate and indirectly in adult morphology). Another general constraint is the ability of embryos to regulate, for example, by the specific mechanism of intercalary mitotic growth in epimorphic systems in metazoans (e.g., vertebrate limbs, dipteran imaginal discs). This resilient mechanism is responsible for establishing pattern continuity at the cellular level during embryogenesis (positional information, "Bateson's Rule," etc.) and for re-establishing this continuity after perturbation (as during regeneration). Interactions of processes seem to be responsible for constraints. Those workers who invoke developmental constraint at the population and specific levels need to avoid ad hoc arguments and attempt more explicit and experimentally based explanations for limits on evolutionary change.

Developmental constraints can provide evolutionary opportunity. The phenomenon of regulation during development simplifies the kinds of evolutionary transitions necessary for the evolution of complex characters. For example, developmental regulation of the peripheral circulation in vertebrates makes changes in the locomotor system possible without concomitant change in the genetic information for the circulatory system.

A major unsolved problem is the absence of operational criteria for the recognition of developmental constraints. If this concept is to have general utility, and not simply invoked in an ad hoc manner, such criteria are necessary.

An area of important disagreement is the biological basis of developmental constraints. Some discussants were willing to concede that constraints might exist if they are ultimately genetic in nature, while others argued that evolutionarily significant constraints are most likely imposed by developmental processes (e.g., epigenetic interactions) that are far removed from the level of the genes.

Strong arguments were made in favor of the organization of a research program in development and evolution that is explicitly genetic, with an emphasis on specific gene substitutions and on mutations of relatively large effect. Others strongly disagreed, arguing that development is not strictly hierarchical, e.g., the same genes are used over and over again. Such workers view the roles of genes as being more generic, with differences in the regulation of developmental timing and interactions, rather than new genes, being responsible for new morphologies. Although there is strong disagreement over whether new molecules and new genes, or reorganizations of existing molecules and genes, are of primary importance in new morphologies, there is considerable agreement that the time has come to emphasize processes over patterns in understanding the interaction of development, phylogeny and evolution.

SYSTEMATICS AND HOMOLOGY

Ontogeny and systematics have been conceptually related ever since the "three-fold parallelism" of the last century: ontogeny, paleontology (time), and comparative anatomy. The perception of this relationship continues to flourish and evolve. There are, however, some fundamental differences in the approach to ontogeny by developmentalists and systematists, and these need to be understood if a commonality of purpose—to link development and evolution—is to be attained.

In order to examine trait or character evolution, developmental biologists rely on systematics for hypotheses of phylogenetic relationships. Only within a phylogenetic context can questions be asked concerning the evolution of ontogenies, the importance of heterochrony, the role of developmental constraints on evolution, and the extent to which developmental processes are coupled or decoupled in evolution. Developmental processes or patterns, or both, must be "mapped" onto a phylogenetic hypothesis and examined by parsimony methods in order to infer ancestral conditions and pathways of change.

Systematic biologists ask how organisms are interrelated. In order to answer this question, characters must be polarized. Ontogenetic information is used by some systematists to distinguish ancestral from derived states, for ordering character state transformations, for determining homologies among adults, and as a source of new character data (i.e., ontogenies used as characters). All of these uses are controversial and under continued study, but there is general agreement that the empirical information that is generated by developmental biologists is of value to systematists.

Homology is the basis of systematic biology. When one asks whether homologous structures can have different ontogenies, an implicit assumption is that the structures in question are those found in adults, i.e., the endpoints of developmental processes. Because no one doubts that nonterminal changes can take place in developmental sequences, it would seem that ontogeny cannot be used as the sole criterion in recognizing homologues, but there is not agreement on this point and some consider common development as the central determinant of homology. Increased emphasis is being placed on whole ontogenies as constituting the relevant characters of systematists. Determining homology among parts of developmental processes for use in phylogenetic reconstruction, however, remains a major and largely unappreciated problem. The issue of homology may be strictly a theoretical issue to many, but it is a matter of central, crucial, pragmatic concern to systematists. Developmental biologists can help by suggesting criteria for individuating or delimiting parts of developmental processes or of ontogenetic trajectories as homologues.

PROSPECTS

The discussion of prospects in the emerging field featured brief statements by many participants on opportunities and difficulties. Some applauded the audaciousness of modern work in developmental genetics, pointing out that we do learn even from sweeping comparisons of yeast, flies, frogs, and humans, as in the case of homeobox genes. Sometimes we need to be bold. But others argued that we are not after universals, but rather differing levels of generality. The issue becomes how to systematize these levels. Variation occurs in development, and the level at which it is investigated is a function of the question pursued and the system under study. Broad comparisons may be appropriate for evolutionarily conservative phenomena. More fine-scaled comparisons are necessary if one is studying the nature of evolutionary transitions at low phylogenetic levels. The incorporation of systematic biological procedures (fundamentally those of phylogenetic systematics) into all parts of the investigation of developmental processes should have a generally salutary effect.

There was lively debate concerning the recent incorporation of quantitative genetic approaches to development and evolution by various workers. Some argued that most quantitative genetic approaches incorporated simplistic assumptions about gene action. Others defended the quantitative genetic approach on the grounds of its empiricism and utility, pointed out the existence of recent theoretical developments, and urged that quantitative genetic models be tested in the context of new genetic discoveries.

One speaker argued that "truth is the intersection of independent lines," and thus argued for diversity in approach. This was echoed by many speakers, who advocated different approaches including: quantitative, developmental and physiological genetics, that would focus on whole phenotypes and connect to phenomena such as pleiotropy and epistasis; molecular developmental genetics, that would focus on molecular genes of large effect; population genetics of development, which may require new formulations; and phylogenetic analyses of ontogenies, which should give deeper and more meaningful insight into character evolution than at present. Modern developmental biology is "full of details," as one speaker put it. Will the evolutionary generalities be found in the details?

Although there was not unanimity of view, a widespread notion was that a new field of evolutionary developmental biology should not be reduced to the functioning of genes. Rather, central questions should be: how development itself evolves, how multicellularity has arisen and what has led to the origin of individualized parts of the phenotype, how developmental processes influence morphological evolution, how appropriate experiments in development can be conducted in a comparative framework, and how an experimental framework can be formulated in an evolutionary and phylogenetic setting. The synthesis of development, evolution and systematics will require knowledge from all fields in areas ranging from theory to experimental design, methods for testing, and analytical procedures. Pursuit of "pure" developmental or evolutionary questions will continue to produce valuable data, but the accumulation of information from such approaches is not necessarily applicable to the questions generated from a synthetic approach.

The enthusiasm generated by the workshop and the spirited debates that took place are clear signs of the vitality of what is a new and exciting area of biology. We are entering, once again, a period of synthesis with respect to evolution. This is not a unification of information from diverse areas of inquiry, but a synthesis of methods, procedures, and analysis combined with new knowledge. It is a time of opportunity and challenge.

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