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ENVIRONMENT, DEVELOPMENT, AND EVOLUTION

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Evolutionary Developmental Biology (EDB) represents a new research agenda that unites evolutionary and developmental approaches to organismal form. In order to succeed, however, this resynthesis of development and evolution must include the environmental effects and physiological (endocrine / homeodynamic) processes that are part of organismal development. Ecology has been slow to embrace this new synthesis. Comparative physiology has been even slower, but there have been calls from funding agencies and leading researchers for an evolutionary comparative physiology. Similarly, with few exceptions, developmental biologists have been slow to embrace environmental and ecological-populational thinking in their approaches, either to development or to EDB. Very little attention has been given to physiological and metabolic processes that could mediate interactions between environ-ment, development, and evolution during ontogenetic and phylogenetic change. It is our contention that it may be environmental and physiological theories, emphasizing dynamic systems and equilibrium properties, that will contribute the next, significant chapter to formulating a true synthesis of evolution, indeed to completing the modern synthesis.

The workshop intends to redress the omissions described above by bringing together a group of leading researchers from quite disparate fields of biology, and working on quite different systems, to examine the interface between environment, development, and evolution, in order to formulate what Scott Gilbert in a recent paper calls "eco-devo," but could be called "eco-evo-devo." The workshop shall show the dynamic interaction between development and other physiological sciences, as well as how environmental signals are translated into change in biological systems. Because the topic requires a hierarchical integration of biological organization, the workshop includes approaches ranging from the molecular/genetic to the population level, and shows how embryonic development relates to life-history evolution, adapt-ation, and responses to environmental factors.

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Abstracts

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Alternative Ontogenies and Evolution

Populations of phenotypes which form a species occur only at various stages of individual ontogenies. A single cleaving cell cannot be in the same stabilized state as a differentiating multicellular embryo or reproducing adult. The entire ontogeny of a phenotype must, therefore, consist of a sequence of stabilized states. It does not progress gradually but proceeds in a saltatory fashion via natural thresholds from one homeorhetic state to the next with increasing complexity and specialization. At times, bifurcations do occur providing alternative stabilities such as more indirect and more direct developments, maintenance or dispersal phenotypes, generalists or specialists. These patterns can all be grouped as altricial and precocial forms. Like the wave particle duality in physics, life processes use bifurcations to create both novelties and alternative answers, as and when required at any interval of ontogeny and evolution. The bifurcations at various times of epigenesis form two different sequences of ontogenetic intervals, one more generalized, the other more specialized, the altricial and precocial homeorhetic states. These are a result of variations which are constantly decreased by the tendency to specialize, and which are channeled via bifurcations into different self-organized stabilized states, until extinction or change become inevitable. The ability to maintain altricial and precocial forms through generations makes it possible to have at any time two answers prepared for unknown future environments. Consequently, if certain changes persist for generations in a stable environment a new evolutionary unit may be stabilized. Examples will be provided.

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Evolutionary Aspects of Thyroid Hormone Effects in Invertebrates

While it is customary to regard the thyroid hormones as characteristic of vertebrate animals, evidence is accumulating that they have a number of effects on invertebrates. Many members of the lower taxa can be triggered to metamorphose by thyroid hormones. Recent results have shown that in insects, thyroid hormones mimic the effects of the juvenile hormones on membranes of follicle cells, and that both JH and TH are capable of binding to the same membrane receptor protein. Similarly, JH mimics the effect of TH on the mammalian red blood cell membrane, and JH competes for a binding site for TH on the red blood cell. It has been known for many years that carbon dioxide can mimic many of the effects of JH. More systematic experiments have suggested that CO_2 mimics the membrane effects of JH and TH on both insect and mammalian tissues. These effects are diminished or blocked by antibodies raised against a putative membrane receptor protein for JH. While the results are still to fragmentary to draw definitive conclusions, they allow us to raise questions about the origin and evolution of membrane receptors for these hormones.

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Induction Beyond the Embryo: Evolution as the Control of Development by Ecology

The first portion of Van Valen's (1973) aphorism — "a plausible argument could be made that evolution is the control of development by ecology" — is often cited but little investigated within the context in which Van Valen evoked it, which was as a contribution to evolutionary theory. A second context is in the identification of a class of evolutionary mechanisms. I will argue for the role of inter- and intraspecific causal links between inductive interactions, ecological adaptation, and evolutionary plasticity in morphology as a mechanistic linking of environment, development, and evolution in what could be called eco-evo-devo. Inductions are the epigenetic interactions between cells (usually epithelia and mesenchyme) that initiate differentiation and morphogenesis of new cells and tissues within individuals. Mostly investigated as embryonic inductions that operate during development, inductions can operate throughout ontogeny or be initiated in adult life. I will argue further that inductive interactions are not limited to ontogeny but occur (a) between individuals of the same species, (b) between individuals of different species, and (c) between species and their biotic and abiotic environment. Examples of each class of inductive interactions will be provided — pheromone-based signaling in social insects and density-dependent interactions in amphibians as examples of intraorganismal induction; interactions between predator and prey as examples of interspecific (predator-prey) interactions; and diet and environmental calcium-induced morphogenesis in moths and fish as examples of environmental inductions. Examples of interactions involving more than one class of inductive signaling will also be discussed. I will show that all three classes of interactions share an ability to activate developmental pathways that initiate new embryonic, larval or adult morphologies. Fundamentally, only the source of the inductive signal differs between these three classes of inductive interactions and mechanisms of evolutionary change.

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A View of Phenotypic Plasticity from Molecules to Morphogenesis

Why have developmental biologists of the last 40 years virtually ignored the impact of environment on development and its implications for evolution? I suggest that phenotypic plasticity in response to environment has been most readily detected in systems mediated by hormonal control and that hormonal control has not been implicated in the early development of animals (the period of most interest to developmental biologists.) If this view is correct, it raises questions concerning the stages and mechanisms most amenable to adaptive changes in the evolution of development.

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Eco-Evo-Devo in Early 20th Century Vienna

In 1902 a remarkable institution was founded in the modernist atmosphere of turn-of-the-century Vienna. The "Biologische Versuchsanstalt", also called "Vivarium", was a private research institute, later incorporated into the Austrian Academy of Sciences, that was devoted entirely to the empirical study of the relationship between environment, development, and evolution. The institute was designed to promote experimentation involving whole organisms and their entire life-cycles over several generations, and under variable environmental conditions. I will discuss the historical background, the research program, its implementation, and some of the results of this unique, scientific undertaking, which ended through the horrors of world war two. I will close on a few notes about the relation of the Vivarium movement to what we now call eco-evo-devo and its role in the conceptualization of modern theoretical biology.

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The Determined Embryo: Homeodynamics, Hormones, and Heredity

At the beginning of the Twentieth Century, when what is now known as developmental biology was called "causal embryology" or "Entwicklungsmechanik", Edwin G. Conklin divided the differing cleavage patterns of embryos into two types: determinate and indeterminate. One hundred years later we speak of variable or invariant cleavage. What has changed, in terms of both our terminology and understanding of these fundamental developmental processes? Now, at the beginning of this Century, in what has been called the "post-genomic era" are we any closer to answering the profound developmental problems (morphogenesis, regeneration, senescence and cancer, to name a few) that intrigued the European and Wood's Hole embryologists? In the early nineteen eighties, Ryuichi Matsuda suggested that the environment (outside) could act on the endocrine system (inside - homeostasis), creating hereditary shifts in timing (heterochrony) by means of genetic assimilation (a la Waddington). About the same time Robert G.B. Reid (1985) posed the problem that there had always existed the "homeostasis paradox", i.e. "If homeostasis is characterized as constancy, and evolution characterized as change, how did the homeostatic condition evolve? To address Matsuda's and Reid's concerns I coined the term "homeodynamics" (1986) by which I meant, "Life history (environment) interlaces with homeostatic and, thus, homeodynamic forces to create the organism's evolution, development, and demise". Further, in defending Matsuda's views I predicted that it would be physiologists that would make the significant breakthroughs in our understanding of evolution. In one way (not the way I had envisioned, however) this has come to pass. Perinatal developmental physiologists have begun to speak of "adaptation-maladaptation syndromes" (see the work of Gluckman, Seckl, and Godfrey). The writing is on the wall, I argue -- evolutionary theorists will have to have a much greater understanding of both the environment and comparative physiology of organisms to remain relevant.

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Epigenetics and Environment: The Historical Matrix of Matsuda´s Pan-Environmentalism

Pan-environmentalism is a synthesis of evolutionary epigenetics and neo-Darwinism, stressing the impact of the external environment, as mediated by the internal milieu of the organism. It allows that processes of epigenetic evolution might be gradual or saltatory. I trace the origins of pan-environmental concepts that Matsuda acknowledged in his writing, and add relevant historical connections that he omitted. A broader environmental context would also comprise symbiotic, physiological and behavioural influences. By theory and experiment, Geoffroy forged the first link between saltatory epigenetics and environment. Bateson tried, but failed to follow through. Some neo-Lamarckists gave epigenetics and environment central roles in evolution. Cope introduced heterochrony, and considered how physiology was changed by the environment. In the early twentieth century, hormonal research, and Kammerer´s experiments, initially boosted neo-Lamarckism. During its decline, theorists such as Goldschmidt continued to ponder evolutionary epigenetics. But Matsuda was not a fan of the hopeful monster. Instead he paid particular attention to Schmalhausen and Waddington on genetic assimilation. Since metamorphosis was also important, he adduced the relevant ideas of Garstang, and De Beer. Julian Huxley´s Modern Synthesis was unsuccessful in advancing epigenetic studies. In contrast, Matsuda´s dialectical synthesis is more relevant to current advances in evolutionary developmental biology, and could be made more comprehensive without compromise.

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The Evolution of Amphibian Metamorphosis: New Insights from Molecular Biology

In his book "Animal Evolution in Changing Environments with Special Reference to Abnormal Metamorphosis", Ryuichi Matsuda attempts to synthesize the roles of environmental, developmental, and genetic factors in the evolution of animal life histories. He gives particular attention to amphibians whose metamorphoses are characterized by numerous changes in tissue arrangement and differentiation, all of which are mediated primarily by thyroid hormone (TH). Amphibians have also repeatedly evolved, in Matsuda's words, "abnormal metamorphoses", meaning large scale transitions in the timing and/or extent of metamorphic remodeling. To explain these transitions, Matsuda extrapolated from current knowledge of amphibian metamorphosis to postulate changes in the production or activity of TH. He proposed that these hormonal changes are induced by environmental stimuli that alter egg or larval development, and are subsequently fixed by genetic mutation and reinforced by natural selection. His hypotheses, however, were formulated prior to the 1986 discovery of the TH receptor gene, which has since triggered an explosion of research into the mechanisms of gene regulation involved in TH production, TH processing, and TH-mediated tissue responses in both amphibians and nonmetamorphic vertebrates. My aim is to glean from this research information to address two questions. Which changes in gene regulation may have been essential to the origin of amphibian metamorphosis, and which mechanisms may be involved in its diversification? By focusing attention on the genetic structure of metamorphic regulation, we may arrive at a better understanding of the manner is which metamorphic ontogenies are shaped by natural selection.

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Conceptualizing Heterochrony: It's Time for Change

Conventional conceptualizations and definitions of heterochronic patterns have been formulated on the basis of a specific mathematical formalism. In this symposium contribution, these conceptualizations

and definitions are shown to be particular cases derivable from a more general mathematical formalism relating ontogeny and phylogeny. The more general formalism provides more precise analytical and etymological descriptions of heterochronic patterns. To exemplify the advantages of this more abstract formulation, a particular heterochronic pattern that involves environmental, evolutionary, and developmental interactions but is unaccounted for by the terms associated with the specific formalism is shown to be accommodated by the general formalism.

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The Origin of Insect Juvenile Hormone and the Regulation of Its Production

The phylum Arthropoda (joint-legged animals) is now believed to be derived from a single arthropod-like ancestor (monophyletic origin), on the basis of both morphological and molecular data. Although the relationships between the classes of Arthropods remain unclear, recent work suggests that the Insecta and the Crustacea (crabs, lobsters, barnacles, and shrimp) are closely related sister groups. It is believed that sesquiterpenoids are the ancestral regulators of reproduction and, only secondarily, of metamorphosis in Arthropods. As physiological regulators the production of these sesquiterpenoids must in itself be regulated by still other signaling molecules. Our recent work on peptides indicates that neuropeptides which regulate juvenile hormone production in insects have arisen on several distinct occasions. It is likely that these peptides occurred originally as regulators of other physiological processes such as modulators of muscle activity or of neurotransmission and were subsequently co-opted for the regulation of sesquiterpenoid biosynthesis. In view of the likelihood that the regulation of reproduction by sesquiterpenoids preceded their role in metamorphosis, regulators of hormone production probably appeared first in adult forms and subsequently in larval forms. Neuropeptides could therefore show two distinct stage-specific functions. The evolution of peptides to assume additional physiological functionality probably occurred through the process of gene duplication and modification at both the peptide and receptor levels. Differences in sesquiterpenoid regulation of reproduction within the insect orders and between the insects and crustaceans suggest that there are numerous peptide regulators of hormone production in the arthropods.

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Eco-Evo-Devo : Perspectives from the Fossil Record

I will discuss evidence that particular kinds of heterochrony have at certain past times appeared in parallel in many lineages, reflecting shared, inherited morphogenetic responses to common environmental causes. For an early example, the currently best-supported argument on the "Cambrian explosion" of animal forms (Fortey et al., 1997) suggests that those lineages had been on earth long before that event, but as minute, softbodied forms, and hence unrecorded as fossils. The "explosion" was one of explosive skeletization, as many lineages in parallel increased greatly in body size, with consequent growth of hard tissues, in response to the same major physical changes. In the Carboniferous, some 300 my ago, giant and morphologically diverse forms appeared in many lineages - from insects to land vertebrates - coincident with a marked increase in atmospheric oxygen. The precise nature and timing of the physical and biotic changes in these early cases is still somewhat shrouded in the mists of time. In contrast, the patterns during the past ten million years have much

better resolution, and closely related living forms can be analytically integrated. These late patterns show that major global cooling trends were associated with suites of coherent changes in many mammalian lineages ranging from rodents through ungulates to hominids. Not only the similarities between the morphological novelties across these mammals suggest that inherited developmental responses to common environmental causes played a major part - whether in the form of directly induced ecophenotypes with subsequent organic selection, or as constrained ontogenetic responses to mutation, or both. Also the differences, which assort coherently between monophyletic groups, indicate that cladistically shared constraints and response capabilities of developmental systems were involved.

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Environmental Effects, Embryonization, and the Evolution of Viviparity

Ryuichi Matsuda hypothesized that changing environments induce patterns of "abnormal metamorphosis", and that environmentally modified phenotypes become genetically fixed. He believed that the hormonal basis of development responds to environmental variation, so that in some groups developmental acceleration occurs, through a process he called embryonization (the incorporation of larval stages in species with small eggs into the period of intra-oval development in large eggs). Derived modes of reproduction in amphibians provide "natural experiments" that test Matsuda's hypotheses. Direct development is an obvious example of embryonization, in that development usually through metamorphosis occurs before hatching; ova typically are large. The evolution of viviparity (specifically defined as provision of maternal nutrition after yolk is resorbed), however, is more complex, and includes an interaction of maternal and fetal hormonal regimes with environmental factors, resulting in the development of small ova, but maternal investment following yolk depletion. Ovoviviparity, the retention of developing embryos that are yolk-dependent, may be an evolutionary step in embryonization. Placental viviparity in some reptiles and nearly all mammals is also evidence of the pattern and process of embryonization. In all taxa studied that have embryonized development, the developmental trajectory is modified relative to that of non-embryonized taxa in the same lineage, perhaps Matsuda's "abnormal metamorphosis". Matsuda's hypothesis provides a useful perspective for the analysis of pattern and process of the evolution of reproductive modes.

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The Impact of Environmental and Hormonal Cues on the Evolution of Metamorphosis as a Labile Developmental Strategy in Lampreys.

Lampreys are one of only two extant representatives of the jawless fishes, the Agnatha, whose ancestry can be traced to the early Cambrian period, about 550 million years ago. Fossils do not provide evidence of whether adult lampreys developed directly from hatched embyros, whether there were precocious (neotenic) larvae, or whether there was a metamorphosis. Among extant lampreys, there are two adult life history types, parasitic and nonparasitic. Present theories indicate that closely related (paired) parasitic and nonparasitic species evolved from a parasitic ancestor. Heterochrony at metamorphosis (influenced by habitat and water temperature) seems to be responsible for polymorphism among some nonparasitic populations resulting in parasitic morphs. When the animals are physiologically prepared, it takes a simple rise in temperature (not the magnitude of the rise) to trigger spontaneous metamorphosis. As in other vertebrate metamorphoses, thyroid hormones are important to lamprey metamorphosis but it is the drop in plasma levels in the latter and not the rise as in the former, that is coincident with the onset of developmental changes. Many years of study of the thyroid and reproductive axes in lampreys has led to two disparate views of the evolutionary timing of metamorphosis. Either metamorphosis appeared early in the Cambrian ancestors of lampreys or it is a relatively recent developmental strategy that was dictated by the environment. Evidence, partially derived from knowledge of the evolution of protochordates, suggests that precocious, marine larvae had highly efficient endostyles for binding iodide and for synthesizing thyroglobulin. A switch to freshwater habitat required a more efficient means of storing iodide in this iodide-poor environment. A follicular thyroid gland was a consequence of an integrated developmental change called metamorphosis. The metamorphosis was a consequence of the high levels of thyroid hormone produced by the larval endostyle. These speculations on a putative history of lamprey metamorphosis under the influence of the environment are supported by experimental evidence.