Evolution and Development

J. T. Bonner, Editor

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Rapporteurs:
I. Dawid · J. C. Gerhart · H. S. Horn · P. F. A. Maderson

Program Advisory Committee:
J. T. Bonner, Chairman · E. H. Davidson · G. L. Freeman
S. J. Gould · H. S. Horn · G. F. Oster · H. W. Sauer
D. B. Wake · L. Wolpert

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NAMING THE CHANGES

No modern subject has dominated evolutionary thought with quite the force that Haeckel’s biogenetic law exerted during the late 19th century (16). Since Haeckel’s law — best known by its tongue-twisting motto, ontogeny recapitulates phylogeny — is fundamentally about change in developmental timing, this reborn theme of the last decade or so has deep, but usually unacknowledged, roots.

Recapitulation cannot work unless development speeds up continually in phylogeny — for adult stages of ancestors must be accelerated in ontogeny to appear in juvenile descendants, thereby making room for the addition of new features to the end of inherited ontogenies. Thus, Haeckel’s law proposes a universality of changing developmental rates in evolution — but all the change is in one direction only: a speeding up. European scientists had known the axolotl since Cortes whipped Moctezuma, but this neotenic salamander was shunted aside as an exception.

With the rise of Mendelian genetics, Haeckel’s law of universal acceleration lost its rationale: if genes make enzymes and enzymes control rates, then slowing down should be as orthodox as speeding up. All styles of change in timing had to be
acknowledged as evolutionary mechanisms. A complete taxonomy of styles must form a basis for any proper analysis.

Borrowing an old word in a new context, evolutionists christened as heterochrony the general phenomenon of change in the timing of development. Classifications of the styles of heterochrony abound ((16), pp. 209-211), but de Beer's (6, 7) classical treatment formed the basis for most discussion, in the English literature at least. But de Beer's taxonomy is cumbersome, incomplete, and inconsistent in places ((16), pp. 221-228); all his complex names reduce to acceleration and retardation, the two faces of heterochrony. (It is important to specify the criterion - size, age, or developmental stage - used as a standard for calculating acceleration or retardation in the development of other structures in descendants vs. ancestors. Different features also speed up or slow down at different rates. This dissociability of features and ambiguity in criteria of standardization have engendered all the complexity and confusion of the classical literature).

Gould ((16), pp. 246-262) devised a "clock model" to obviate these difficulties, but it was incomplete and insufficiently quantified to rank as an adequate formalism for heterochrony. Alberch et al. (1) have devised a complete and operational system. It renders all the phenomena of heterochrony as consequences of positive or negative perturbations in three parameters: onset signal, offset signal, and growth rate. All the old names of de Beer's system lead to one of two morphological expressions in descendants vs. ancestors: paedomorphosis, or the appearance of ancestral juvenile structures at later stages of descendants, and peramorphosis, or passage through the ancestral adult stage to new extensions or modifications.

This formalism may sound excessively lawyerly, but the previous lack of a rigorous framework has spawned 200 years of squabble and incomprehension and has led to the common impression among evolutionists that this subject is both arcane and unprofitable.

With the Alberch et al. model, we can look at any example of change in developmental timing and (if we have adequate information) specify the processes that produced it. For example, increase in the complexity of ammonite sutures in lineage after lineage is one of the most conspicuous evolutionary trends noted by paleontologists. Newell (23) graphed an example in a lineage of Paleozoic ammonoids by plotting sutural length against shell diameter in the traditional log-log format of allometry. Allometry is positive in the ontogeny of all genera, and sutures continually increase in relative length (and therefore in complexity of folding). The descendant lineage has both a higher slope and a higher y-intercept than the ancestor; it also reaches a larger adult size. This classical example of "recapitulation" (increasing sutural complexity by passage through the ancestral adult stage at a juvenile stage in descendants) is a result of all three possible processes leading to peramorphosis: 1) Positive displacement of offset. The lineage exhibits phyletic size increase and sutural allometry continues beyond the size of ancestral adults. 2) Increase in growth rate. Rise of the allometric slope indicates that the suture lengthens relatively more rapidly in descendants. 3) Negative displacement of onset. The two curves converge but do not join at the initial post-embryonic size. The higher y-intercept of descendants indicates that the suture, at its initial appearance, was already longer than the ancestor's at a comparable stage.

QUANTITATIVE EFFECTS ON MORPHOLOGY
The inputs to heterochronic change are simple quantitative alterations in rate and timing of underlying processes that generate altered morphologies. The fascination of the subject has always resided in the conviction that apparently complex changes in morphology might be reduced to such simple graded causes (see (29)) and modern computerizations of the same theme (26, 30).

Often, however, simple inputs translate to simple outputs, and the evolutionary effect of a small change in timing is a small alteration in morphology in the same, predictable direction.
Changes in this category have spawned an immense literature, generally gathered under the heading of allometry (5, 12, 15, 18). Scores of allometric changes have been documented for all three parameters of Alberch et al. model of heterochrony. For example: 1) Displacements of offset signals. Phyletic size increase (Cope’s rule) is a common, but frustratingly unexplained, phenomenon in evolutionary lineages. Many famous evolutionary trends in morphology represent little more than a simple extension along previous allometric trajectories into enlarged ranges of body size. Sinnott showed long ago (28) that many of the more bizarre and twisted forms of bottle gourds arose by simple allometric extension from rather ordinary shapes of smaller relatives. Gould (14) studied static allometry among adults of the Irish Elk (Megaceras giganteus) and found that its celebrated antlers could be a correlate of increased body size, given the pervasive positive allometry of antler size in ontogenetic and static allometry of deer. 2) Displacements of onset signals. Ontogenetic allometries of common slope, altered y-intercept, and similar range of body size record changes in the time of onset for the ordinal variate (13). This style of allometry, though not as widely discussed as other categories, is actually quite common. It formed the basis of Dubois’ original work on the subject during the 1890’s (allometry of brain size in mammals) and has been especially pursued by German allometricians under the heading of Transpositionsallometrie (see (24)). 3) Changes in growth rates. The bulk of the allometric literature records changes in slopes of double log plots, leading to a modification of the relative growth rate for the allometric variable vs. body size. In an example close to home, Pilbeam and Gould (25) showed that a change to positive allometry from the virtually universal negative allometry of brains in phyletic series obeying Cope’s rule could account for the large brain of Homo sapiens.

Although allometric cases could be catalogued by the hundreds, it is not clear that they qualify, under the subject of this paper, as a “mechanism of macroevolution.” They arise as a result of change in developmental timing, but they produce a small quantitative output for a small quantitative input. As such, they enter the evolutionary process as minor variants, as Darwinian raw material for scrutiny by natural selection. They are no different from other small variants and do not impart any special character to macroevolution.

Development has a special “relevance” to macroevolution insofar as it imposes styles of evolution departing from the extreme Darwinian notion that virtually all change is a result of natural selection working on a spectrum of small, random variation. Under this strict selectionism, all evolution can be smoothly extrapolated from allelic change in local populations, and development plays little role beyond purveying some of the variation that natural selection requires as raw material. Development can have direct input to macroevolution in two major circumstances: 1) if it constrains variation in such a way that the materials presented to natural selection are not random and if, therefore, the path of evolutionary change is in part determined by limited inputs; 2) if it provides major variants that lead to a saltatory (and constrained) alteration of phenotype, at least for certain “key characters” of evolutionary transitions.

The allometric variants, although small and graded as their inputs, might still have relevance to macroevolution under the first criterion above— that is, if they constrain available variation and impart a preferred direction to evolutionary change not based upon natural selection (but upon systems of covariation in development). I believe that allometry plays an important role in macroevolution in this sense, but that it has not been sufficiently recognized because we tend to interpret all changes in adaptive terms, even when our arguments cannot transcend the speculative. For example, a large literature exists on the putative adaptive significance of reduced hair covering in humans (19). Virtually all of it assumes that reduced body hair is a direct result of natural selection.
working for this explicit result from a spectrum of random variants. Yet reduced hair in precisely the places we conserve it (capillary, axial, and pubic) is the expectation of neoteny in human development - for it represents the fetal pattern of other anthropoids. We may use it secondarily for some adaptive purpose, but the phenomenon itself may be a direct consequence of change in developmental timing (neoteny) adaptive for other reasons. Similarly, Alberch (3) has shown that interdigital webbing and reduction of phalanges arise again and again - and are surely adaptive - in independent lineages of bolitoglossine amphibians. But an extreme Darwinian explanation would not tell the whole tale. For these features arise in lineages of reduced body size and are paedomorphic consequences of the reduction. They work well, but their repeated appearance may record the constraints of variation arising from developmental programs more than the meticulous scrutiny of ubiquitous variation by natural selection. Many classic cases of convergence may have to be reinterpreted more as results of limited (albeit adaptive) variation than as multiple, unconstrained approaches to mechanical optima. Did the ichthyosaur "dorsal fin" really arise from nothing, or might it be (despite its lack of internal structure) the homolog (based on inherited embryological potential) of a fully-developed, distant ancestral feature?

Granting to allometric variants this role as constrainers in macroevolution, the subject of change in developmental timing still exerts its major fascination through the claim that small inputs might lead to large and surprising outputs. We take up this subject in the last section after a short comment on genetic bases.

A NOTE ON THE GENETIC BASIS OF LARGE PHENOTYPIC EFFECTS ARISING DISCONTINUOUSLY

Of the various mechanisms proposed by Goldschmidt (11) for the origin of "hopeful monsters," only small genetic changes producing large effects by altering rates of development in early ontogeny (with accumulating and cascading results thereafter) have any claim to theoretical validity.

Several population geneticists, Lande in particular (20), have vigorously denied the evolutionary importance of such a phenomenon, arguing that although such mutants are common enough as pathological variants, the genetic basis of all species differences that might putatively be assigned to such an underlying cause is highly polygenic - even though the morphological transition may be abrupt, as a threshold effect. But Sewall Wright (31), though generally supporting Lande on the evolutionary unimportance of macromutations, points out that the current polygenic basis of characters in long-established, successful species need not reflect their mode of origin. Characters initially arising as large effects of single mutations would probably be poorly canalized and therefore subject to later stabilization through the selection of modifiers - thus establishing a subsequent polygenic basis.

Unfortunately, we know disappointingly little about the genetic basis of most allometric and heterochronic events whose phenotypic effect has been documented. We do not even know, in the most famous case of all, whether "who does and who doesn't" in the facultative paedomorphosis of ambystomatid salamanders has any genetic basis behind it. A simple genetic foundation has, however, been documented for some continuous allometries and heterochronies (in gourds (28), and Ford and Huxley's classical experiments (9) on eye color in Gammarus) and for some discontinuous effects as well (Cock (5), on creeper vs. ordinary fowl and Bell (4), on three heterochronically based adult morphs of stickleback fish).

Although this lack of information is disappointing (and we would not wish to be a Philistine and declare the subject unimportant on its own level), in one sense - or at one level in the evolutionary analysis of morphology - it does not matter whether discontinuous phenotypic transformations have a single, oligo, or polygenic basis (see (2), and Alberch, this volume). The discontinuity in itself and the non-existence or even the impossibility of intermediate forms (see (10) on the split maxilla of bolyerine snakes),
whatever their underlying basis, are the enlightening phenomena. For they illustrate the existence of thresholds and prove that discontinuous outputs (whatever the input) are, given the nature of developmental programs, a predictable macroevolutionary phenomenon. In this sense, development is an indispensable consideration in macroevolutionary studies because the constraints that it imposes upon the nature of phenotypic change guarantee that small and continuous Darwinian variation is not the raw material of all evolution. If development constraints and channels variation and imposes discontinuities in variation as well, then it is an evolutionary force in its own right and not just a contributor to the random pool of small-scale variation that makes natural selection the only force of evolutionary change.

SMALL INPUTS, BIG OUTPUTS
Small changes in the timing of developmental events (whatever their genetic basis) sometimes lead to discontinuous changes in phenotype, not just to graded quantitative outputs. When this happens, development may have a direct effect upon macroevolution (as L.S. Berg, A.N. Severtsov, R. Goldschmidt, and others argued forcefully earlier in our century). The new morphology often requires the designation of a new higher taxon, and while selection must fix it by eliminating other variants in the population, its discontinuous origin relegates selection to a negative role (eliminating the unfit) and assigns the major creative aspect of evolution to variation itself. This subject, therefore, poses the greatest challenge (among the themes of our conference) to a strict Darwinism that views all evolutionary change as the product of natural selection working upon small, random variants. The reasons why small changes in timing can lead to large alterations in phenotypes are varied. They include:

1) Discontinuities in ontogenetic programs. In the simplest case, graded inputs lead to graded outputs, but ontogeny itself is discontinuous (rather than allometrically smooth in its morphological changes). A small negative displacement in offset signal may lead to a truncation of ontogeny at a just barely subadult stage, but if ontogeny includes a profound metamorphosis to adulthood, the new paedomorphic adult — that is, the "promoted" subadult stage of the ancestor — will be a profoundly different animal from its parents.

The classic examples of recapitulation are mostly of the continuous type considered in the section on "Naming the Changes" — small additions to the ends of ancestral ontogenies — but virtually all the classic cases of its heterochronic opposite, paedomorphosis, lie within this category of discontinuity. What is an axolotl, after all, but a previously subadult stage, "promoted" virtually in toto. Indeed, most of the macroevolutionary literature on paedomorphosis — a largely useless and highly speculative literature in my opinion, but a large one nonetheless — involves "stories" about how promoted subadult stages may become new classes or phyla: vertebrates from tunicate tadpoles, insects from myriapod larvae, ctenophores from Müller's larva of turbellarians.

2) Dissociability among covariant sets. If every small truncation of development merely promoted a complete juvenile stage to adulthood, then the full potential of developmental programs to initiate major changes would not be realized. For a juvenile stage, however different from its adult, is still part of an animal's normal morphology. Yet I was struck in doing a survey of all ecological situations favoring extreme truncation of development with major reduction of body size in evolution — interstitial habitats, extreme r-selezione, etc. — that tiny descendant adults are never simply ancestral juveniles with mature gonads (16), Chapter 9). When precocious maturation leads to an extreme truncation of ontogeny, some features remain behind in the juvenile stage, but others co-vary with the reproductive organs themselves and produce a new and interesting mixture of ancestral juvenile and adult features in the progenetic descendant. Features of an organism
are bound (often quite loosely) in covariant sets, and these sets are often dissociable as blocks. Some are strongly tied to maturation, others independent of it. Thus, each case of progenesis becomes an experiment in form, not just an integral juvenile stage suddenly able to reproduce. The tiny progentetic veneracean clam Turtonia minuta, 1 to 2 mm long and virtually identical in external form with the spat of Venerupis, has an adult ligament, but larval gills and siphons (24). The dwarf males of the sand crab Emerita are predominantly miniaturized adults, but have larval antennae and pleopods (8).

3) The hierarchical or compartmentalized nature of the genome. This important subject has been treated more extensively by others at this conference (and my category 2 is a subsection of it), but the hierarchical character of genomic action lies behind the possibility of large outputs from small inputs - for a small change in a high-level regulator may affect a continually ramifying and expanding set of developmental processes under its control. Many of these small changes are alterations in rate. The most famous cases are found, of course, in the homeotic mutations of Drosophila. Consider Lewis' model (21) for the action of the 8 BX-C genes as regulators of the structural genes that build thoracic and abdominal segments. He believes that, in normal development, these genes are derepressed in sequence, leading to a gradient in their product increasing from the third thoracic segment to the posterior end of the animal. The more gene product, the more posterior in appearance the form of a resulting segment. Many homeotic effects in the bithorax complex are then produced by changes in rate in this sequence of derepression. In the extreme case, all BX-C genes turn on at once and all segments affected by them differentiate as eighth abdominals.

4) Latent capacities of the genome. If all that the genome could produce were manifest in the realized ontogeny of animals, then we might be able to predict all heterochronic effects, and their range would be limited. But the genome embodies an extensive set of latent capacities, some the echoes of distant ancestors, others, no doubt, the accidental byproducts of physical structure. Small changes in rates often activate these potentials, and the result is not only a surprise, but often a major one.

Atavisms are the best known and most intriguing phenomena in this class. An acceleration in the rate of development for side splits in horses' legs does not simply produce larger splints, but may actually reproduce the original side toes of which the splints are vestiges. In Hampe's famous experiment (17), an increased rate of fibular growth did not only produce a larger fibula, but recreated an ancestral pattern in ankle bones below - since the fibula, which never reaches the ankle bones in normal development of chicks, apparently still retains its ancestral capacity to induce some differentiation in the ankle bones. As Darwin wrote in his Variation of Animals and Plants Under Domestication (1868):

On the doctrine of reversion [atavism]...the germ becomes a far more marvellous object, for, besides the visible changes which it undergoes, we must believe that it is crowded with invisible characters...ready to be evolved whenever the organization is disturbed by certain known or unknown conditions.

The common lesson in all four points holds that organisms are not pieces of putty, infinitely moldable by infinitesimal degrees in any direction, but are, rather, complex and resilient structures endowed with innumerable constraints and opportunities based upon inheritance and architecture (both molecular and morphological). One may be excused for retorting: "so what else is new?" Has any biologist ever denied it? But there is an enormous difference between explicit statement and actual practice. Organic integrity always received lip service, but in a subtle, yet pervasive way, the strict construction that Darwinism has sometimes received in recent times has encouraged us to put this truth on the back shelf and to
consider development primarily as a source for the unconstrained, small, random variants that provide raw material only and make natural selection the sole directing force in evolution. And this subtle emphasis explains why so many fine embryologists, from Berrill to Waddington, were never comfortable with the modern synthesis (see (22) for history and definition of the modern synthesis). Progress in science often demands the recovery of ancient truths and their rendering in novel ways.

REFERENCES

List of Participants

ALBERCH, P.
Museum of Comparative Zoology
Harvard University
Cambridge, MA 02138, USA
Field of research: Evolutionary theory and morphogenesis

BERKING, S.
Zoologisches Institut
Universität Heidelberg
Fachrichtung Physiologie
6900 Heidelberg, F.R. Germany
Field of research: Control of morphogenetic processes in hydra

BONNER, J.T.
Department of Biology
Princeton University
Princeton, NJ 08544, USA
Field of research: Social organization of cells and organisms, developmental and evolutionary aspects

BOTTEN, R.J.
Kerckhoff Marine Laboratory
Corona del Mar, CA 92625, USA
Field of research: Molecular biology of evolution

COOKE, J.
Division of Developmental Biology
National Institute for Medical Research
London NW7 1AA, England
Field of research: Pattern formation in early embryonic development of vertebrates, including genesis of selective nerve connections

DAVIDSON, E.H.
Division of Biology
California Institute of Technology
Pasadena, CA 91125, USA
Field of research: Molecular biology of development

DAVID, I.
Bldg. 37, Room 4D-06
National Institutes of Health
Bethesda, MD 20205, USA
Field of research: Developmental biology, organization and function of the eukaryotic genome

DOHERY, W.
Institut für Allgemeine Zoologie
Freie Universität Berlin
1000 Berlin 33, F.R. Germany
Field of research: Comparative embryology of arthropods (Myriapods, Crustacea), phylogenetic relationships of arthropod groups, ecology of Cladocera

DOVER, G.A.
Department of Genetics
University of Cambridge
Cambridge CB2 3RH, England
Field of research: Evolutionary changes in the genomes of closely related species (Drosophila, Tsetse rodents)

FREEMAN, G.L.
Department of Zoology
University of Texas
Austin, TX 78712, USA
Field of research: Developmental biology

GALLWITZ, D.F.
Physiologisch-Chemisches Institut I
Universität Marburg
3550 Marburg/Lahn, F.R. Germany
Field of research: Structure of eukaryotic genes, evolution of the actin gene

GARCIA-BELLIDO, A.
Centro Biología Molecular CSIC
Universidad Autonoma
Cantoblanco
Madrid 34, Spain
Field of research: Developmental genetics