DEVELOPMENTAL SYSTEMS AND
EVOLUTIONARY EXPLANATION*

F ew scientific ideas are so well embedded in popular culture as the idea that certain features of an organism are genetically determined, while others are acquired by interaction with the environment. There have been many attempts to recast the special role of the genes in an attempt to do justice to our knowledge of developmental processes. The division of traits into innate and acquired has been replaced by attempts to determine the relative influence of genetic and environmental factors on each trait. The idea of an genetically specified outcome has been replaced by a genetic blueprint and then by a genetic program. But all these accounts presume that the key to understanding development is to understand the interaction of two classes of developmental resources—genes and the rest. They are all *dichotomous* accounts of development.

Developmental systems theory rejects the dichotomous approach to development. The genes are just one resource that is available to the developmental process. There is a fundamental symmetry between the role of the genes and that of the maternal cytoplasm, or of childhood exposure to language. The full range of developmental resources represents a complex system that is replicated in development. There is much to be said about the different roles of particular resources. But there is nothing that divides the resources into two fundamental kinds. The role of the genes is no more unique than the role of many other factors.

Many authors have contributed to the developmental systems, or constructionist, tradition in the study of development.[1] We have drawn on this tradition, and particularly on the work of Susan Oyama, to produce a general account of development and evolution. We have tried to confront one major weakness of previous presentations of the developmental systems idea—the lack of any way of delimiting and individuating developmental systems. We suggest an etiological solution: the developmental system consists of the resources that produce the developmental outcomes that are stably replicated in that lineage. By adopting this definition, we bring out the radical implications of the new approach to development for the theory of evolution. The developmental system goes far beyond the traditional phenotype, yet all its elements are parts of the evolutionary process. We argue that a reformulation of evolution in developmental systems terms maximizes the explanatory power of evolutionary theory.

The implications of the developmental systems approach are enormous. In the later part of the paper we try to sketch some of these. We argue that evolution is best construed as differential replication of total developmental processes or life cycles. We show that the well-known distinction between replicators and interactors is no longer of any great use in clarifying thought about evolution. Finally, we suggest that the developmental systems view makes it impossible to maintain the distinction between biological and cultural

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[1] D. S. Lehrman, "Critique of Konrad Lorenz's Theory of Instinctive Behaviour," *Quarterly Review of Biology*, XXVIII (1953): 337–63; "Semantic and Conceptual Issues in the Nature-Nurture Problem," in his *Development and the Evolution of Behaviour* (San Francisco: Freeman, 1970): 17–52. G. Stent, "Strength and Weakness of the Genetic Approach to the Development of the Nervous System," in *Studies in Developmental Neurobiology*, W. M. Cowan, ed. (New York: Oxford, 1981). R. C. Lewontin, *Human Diversity* (New York: Scientific American, 1982); "The Organism as the Subject and Object of Evolution," *Scientia*, CXVIII (1983): 65–82. Oyama, *The Ontogeny of Information* (New York: Cambridge, 1985); "Ontogeny and the Central Dogma," in *Systems and Development*, M. R. Gunnar and E. Thelen, eds. (Hillsdale, NJ: Earlbaum, 1989). M. W. Ho, "Heredity as Process," *Rivista di Biologica-Biology Forum*, LXXIX (1986): 407–47. Johnston, "The Persistence of Dichotomies in the Study of Behavioral Development," *Developmental Review*, VII (1987): 149–82. Johnston and G. Gottlieb, "Neophenogenesis: A Developmental Theory of Phenotypic Evolution," *Journal of Theoretical Biology*, CXLVII (1990): 471–95. H. F. Nijhout, "Metaphors and the Role of Genes in Development," *Bioessays*, XII (1990): 4410–46. Gray, "Death of the Gene: Developmental Systems Strike Back," in *Trees of Life: Essays in Philosophy of Biology*, Griffiths, ed. (Boston: Kluwer, 1992): 165–209. L. Moss, "A Kernel of Truth? On the Reality of the Genetic Program," in Hull, M. Forbes, and K. Okruhlik, eds., *Philosophy of Science Association Proceedings*, I (1992): 335–48.

evolution. Both traditional processes are rejected in favor of a single, richer account of the replication of total developmental systems.

I. INNATENESS, GENETIC INFORMATION, OTHER CONFUSIONS

An early contribution to the development of developmental systems theory was Daniel S. Lehrman's attack on Konrad Lorenz's 1930s conception of innateness (*op. cit.*). The collapse of this conception, and of the idea of genetic information with which Lorenz replaced it, show the fundamental problems with dichotomous views of development.

Lorenz had described an innate trait as one whose origins are to be understood in terms of adaptation during evolution, and whose emergence is insensitive to environmental variation. Learned traits, on the other hand, are to be understood in terms of the organism's adjustment to its local environment, and are sensitive to variation in that environment. Lehrman pointed out that there is no conceptual link between the evolutionary and developmental elements of Lorenz's innateness concept, between the fact that a trait is an evolutionary adaptation and the fact that it is insensitive to environmental variation. It is of no evolutionary consequence whether a trait is sensitive to environmental variation, as long as the actual historical environment regularly provides the required input. "Nature selects for outcomes,"[2] and is indifferent to how they are achieved.

Lehrman supplemented this conceptual point with a host of examples of the role of environmental input in the production of evolved traits. The female rat abstains from eating her young, for example, only if she licks her genitalia during pregnancy. She will construct a nest and retrieve the young only if she has been exposed to temperature variations earlier in her life and had the chance to carry other objects around in her mouth.[3] A later example of the same kind, due to Gilbert Gottlieb,[4] makes the same point. Under normal developmental conditions, young ducklings develop a preference for the maternal call of their own species. Gottlieb discovered that they fail to develop this preference when devocalized in the egg. Exposure to their own prenatal call is required for the development of their preference for the (quite different) maternal call. Lehrman was at

[2] Lehrman, "Semantic and Conceptual Issues in the Nature-Nurture Problem," p. 28.

[3] "Critique of Konrad Lorenz's Theory of Instinctive Behaviour," pp. 342–3. The last two points are disputed by Lorenz in his *Evolution and the Modification of Behavior* (Chicago: University Press, 1965).

[4] "Roles of Early Experience in Species-specific Perceptual Development," in *Development of Perception*, R. N. Aslin, J. R. Alberts, M. P. Petersen, eds. (New York: Academic Press, 1981), pp. 5–44.

pains to point out that these sorts of facts do not show that all traits are "learned," as opposed to innate. They show that reliable developmental outcomes occur because of reliable interactions between the developing organism and its environment. The fact that a trait has an evolutionary history has no implications about the role of environmental factors in the process by which it develops, except that the process is sufficiently reliable to produce similar outcomes in each generation.

In his later work, and partly in response to this critique, Lorenz eschewed the idea that some phenotypic traits are innate, while others are learned. We have found it hard to convince some philosophical devotees of Lorenz that he ever held this "naive" view, but we can hardly do better than to quote his own words. Lorenz noted that his earlier "atomistic attitude" of conceiving complex behaviors as chains of elements, some of which were innate and some acquired, "was a serious obstacle to the understanding of the relations between phylogenetic adaptation and adaptive modifications of behaviour. It was Lehrman's (1953) critique which, by a somewhat devious route, brought the full realisation of these relations to me" (*op. cit.,* p. 80). Lorenz replaced his distinction between innate and acquired traits with a distinction between two sources of developmental information. Some of the information manifested in an organism's adaptation to its environment is phylogenetic, as opposed to ontogenetic. Phylogenetic information is transmitted in the genes, whereas ontogenetic information is gathered from the environment during development. Lorenz's classic experimental paradigm, the deprivation experiment, which was originally intended to reveal innate traits, was interpreted in this later work as revealing the presence of phylogenetic information. A rat reared in isolation and given no opportunity to practice maternal skills nevertheless constructs a species-typical nest, and retrieves its young in the species-typical manner. Lorenz argues that this can only be explained by the genetic transmission of phylogenetic information: "certain parts of the information which underly the adaptedness of the whole, and which can be ascertained by the deprivation experiment, are innate" (*op. cit.,* p. 40).

Lorenz admits that the deprivation experiment does not remove all sources of environmental input. No trait can develop without input from the environment. Trivially, the organism must eat if it is to grow. Less trivially, the rat must have experienced temperature variation and carrying things. The rationale of the deprivation experiment therefore requires a distinction between two sorts of environmental input, those which provide ontogenetic information for

"learning," and those which provide mere physical "support" for the reading of phylogenetic information.

> No biologist in his right senses will forget that the blueprint contained in the genome requires innumerable environmental factors in order to be realised. . . . During his individual growth the male stickleback may need water of sufficient oxygen content, copepods for food, light, de-tailed pictures on his retina, and millions of other conditions in order to enable him, as an adult, to respond selectively to the red belly of a rival. Whatever wonders phenogeny (sic) can perform, however, it can-not extract from these factors information that simply is not contained in them, namely the information that a rival is red underneath (*op. cit.,* p. 37).

This information, therefore, must be contained in the genome, which "rules ontogeny." Lorenz compares the roles of genome and environment in ontogeny to an architect's plan and the bricks and mortar in a building project (*op. cit.,* p. 42). Of all the resources that are utilized in the development of traits that represent phylogenetic adaptations, only one, the genome, provides information. The others merely provide raw materials.

Unfortunately for Lorenz, no suitable notion of information ex-ists which will allow him to draw this distinction between the role of the genome and the role of other developmental resources. Timothy Johnston makes this point very clearly (*op. cit.*). We have a well-understood, mathematical notion of information, derived from com-munication theory. An event carries information about another event to the extent that it is correlated with that event. The "trans-mission" of mathematical information is a matter of the systematic dependence of one system on another. In a classic example of learn-ing, such as a rat finding out which foods are poisonous, there is just such a systematic dependence between the state of the environment and the later state of the organism. After learning, the internal state of the rat carries information about the state of the world. Informa-tion about the food has been transmitted to the rat. But in what Lorenz characterizes as the "maturation" of an innate trait, there is an exactly similar dependence. Lehrman's original examples docu-mented the ways in which developmental outcomes are contingent on the occurrence of interactions with the environment. The devel-opment of maternal care in the rat requires interaction with temper-ature variations, and with material that can be transported. Removal of these factors is reflected in changes in the phenotype, so they must be transmitting information to the phenotype. At the molecu-lar level, cellular differentiation is dependent on a host of extragen-

omic factors. Induction of lactation in mammary cells in mice, for example, depends on the shape of the cells, which is in turn a function of the substrate to which they are attached.[5]

This symmetry between different causal factors in development is intrinsic to the concept of mathematical information. In the Lorenzian picture of "maturation," the nongenetic developmental factors constitute the channel conditions under which the organism carries information about its genes, whereas in Lorenzian "learning" the intrinsic organization of the organism constitutes channel conditions under which the state of the organism carries information about environmental factors. But it is always possible to reverse the roles of the sender and channel conditions. So it is equally open to us to interpret the maturation case as one in which the genes constitute channel conditions under which the organism carries information about some nongenetic developmental factor. We could also interpret the learning case as one in which the environmental factors are channel conditions under which the state of the organism tells us about its genes.[6]

Lorenz's failure to appreciate this symmetry shows us that he did not conceive of genetic information in terms of systematic dependence. Instead, he relied on some intentional or semantic conception of information. When the channel conditions are altered, the genes do not carry different information about the phenotype, they are just misinterpreted. Under abnormal developmental conditions, the phenotype misrepresents its genes. In fact, there are only two ways to make sense of the notion of information in development. First, the entire set of developmental resources, plus its spatiotemporal structure, may be said to contain information about evolved developmental outcomes in the unproblematic, mathematical sense of systematic dependence. But as long as we confine ourselves to this notion of information, there is no causal asymmetry in the role of different resources which makes it legitimate to regard some of them as carrying the information and the others as merely providing conditions in which it can be read. The second, more practical way to make sense of the notion of information in development is to to embed the information in one resource by holding the state of the other resources fixed as channel conditions under which

[5] Moss, op. cit.
[6] A perfectly practical proposal given the extensive literature on species-specific patterns of associative learning. See, for example, M.E.P. Seligman and J. L. Hager, eds., Biological Boundaries of Learning (New York: Appleton, Century, Crofts, 1972).

that information is transmitted. But this move can be used to inter-
pret any of the resources as the "seat" of the information guiding
development, and so it, too, fails to generate the traditional asym-
metry between genetic and other factors.

Our critique of Lorenz can be applied to even the most sophisti-
cated reconstruction of the idea that genes "code for" phenotypic
characteristics. Kim Sterelny and Philip Kitcher[7] claim that a stretch
of DNA codes for a trait relative to a "standard" background of
other genes and a "standard" environment. Given these back-
ground conditions, changes in the gene are systematically linked to
changes in the phenotypic trait. But consider the DNA in an acorn.
If this codes for anything, it is for an oak tree. But the vast majority
of acorns simply rot. So 'standard environment' cannot be inter-
preted statistically. The only interpretation of 'standard' that will
work is "such as to produce evolved developmental outcomes" or
"of the sort possessed by successful ancestors." With this interpre-
tation of 'standard environment', however, we can talk with equal
legitimacy of cytoplasmic or landscape features coding for traits in
standard genic backgrounds. No basis has been provided for privi-
leging the genes over other developmental resources.

II. TAKING DEVELOPMENT SERIOUSLY

Developmental systems theory provides an alternative explanation
of transgenerational stability of form. As Oyama argued in "The
Ontogeny of Information," species-typical traits are constructed by
a structured set of species-typical developmental resources in a self-
organizing process that does not need a central source of informa-
tion. Some of these developmental resources are genetic, others,
from the cytoplasmic machinery of the zygote to the social events
required for human psychological development, are nongenetic.
The spatio-temporal disposition of the resources is itself a critical
resource, as it helps induce self-organization. The fact that appropri-
ately structured resources are available can receive an evolutionary
explanation. The processes which effectively replicate themselves
are those which find appropriately structured resources in each gen-
eration. An extended notion of inheritance, which stresses the role
of past generations in structuring the developmental context of
their successors, is thus a critical part of the theory.

The theory does not deny that there are distinctions among devel-
opmental processes. For example, Gottlieb[8] suggests that different

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[7] "The Return of the Gene," this JOURNAL, LXXXV, 7 (July 1988): 339–61.
[8] "Conceptions of Prenatal Development: Behavioural Embryology," *Psycholog-
ical Review*, LXXXIII (1976): 215–34.

kinds of interactions may either facilitate, induce, or maintain devel-
opmental differences (Patrick Bateson[9] notes that these distinctions
are applicable indifferently to the roles of genetic and nongenetic
factors). But the theory does deny that there are two fundamental
kinds of developmental resources, genes and the rest, and that these
two types play fundamentally different roles in development. It
makes no more and no less sense to say that the other resources
"read off" what is "written" in the genes than that the genes read
off what is written in the other resources. The reading of the genes
is a metaphor which has been of some historical utility, but which
now retards the study of development, and, we shall argue, of
evolution.

Perhaps the best metaphor for development is that of Stent (*op.
cit.*), who compares development to an idealized model of ecological
succession. When an area of ground is denuded of its biota, the
characteristic landscape of that region is re-established in a series of
stages. Adventitious first colonizers, able to survive in the barren
conditions, take advantage of the lack of competition to occupy the
area. Their presence modifies factors such as the soil and microcli-
mate, making the area hospitable to the next phase of vegetation,
and so forth. In this process, as in development, an outcome is
replicated without any blueprint or program, as a consequence of
the presence of the same developmental resources. There is no
room for any distinction between some resources that contain the
information and others that "read it" or "provide the material con-
ditions for its realization." Nor is it possible to bypass a detailed
analysis of the developmental process by going straight to the
sources of the "information" that is "expressed" in the outcome.

The differences between the notion of information that is legiti-
mate in this context and the everyday notion based on our experi-
ence of language is so great that it is very hard not to revert to the
later notion, with all its inappropriate implications. It is perhaps for
this reason that developmental systems theorists, and especially
Oyama (*op. cit.*) have eschewed the traditional metaphor of evolved
traits being "transmitted" from one generation to another. The pic-
ture that we have tried to convey with the metaphor of ecological
succession is much better conveyed by saying that that species-
typical traits are reconstructed in the next generation by the interac-
tion of the same sorts of developmental resources that were present

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[9] "Genes, Embryology and the Development of Behaviour," in *Animal Be-
haviour: Genes, Development and Learning,* P. Slater and T. Halliday, eds. (Cam-
bridge: Blackwell, 1983): 52–81.

in earlier generations. Oyama has also suggested that it is misleading to talk of the information used to reconstruct the phenotype being "transmitted." The resources that construct later stages of the developmental process are constructed by earlier stages. In Oyama's preferred terminology, information is itself the product of an ontogeny.

Figure 1 shows the developmental systems conception in diagrammatic form. A developmental process is reconstructed through the interaction of suitably structured resources. Some, including the genes, are created by the immediate precursors of the generation in question. Others are generated over different periods of time by the collective activities of the population. Others, to be discussed below, persist without reference to these activities. A developmental process "inherits" all these resources. Finally, many vital resources in development are generated by earlier stages of the developmental process itself.

III. INDIVIDUATING DEVELOPMENTAL SYSTEMS

For obvious reasons, even the most systematic presentations of developmental systems theory (for example, Oyama and Gray) have been more concerned to incorporate neglected elements into the

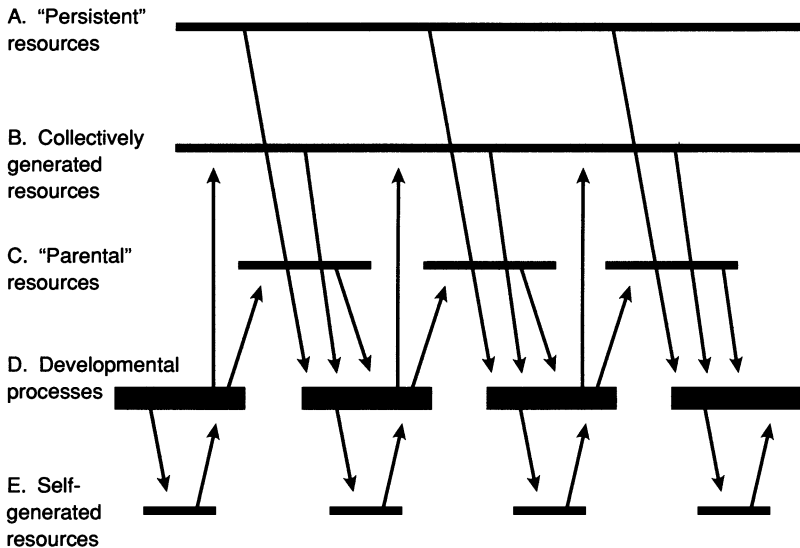

Figure 1. Causal influences in four asexual generations of a lineage of developmental processes. Each arrow represents multiple inputs. Influence of each resource is contingent on the presence of the others. The effects of temporal order of interaction have been overlooked. The broad categories of resources are not intended to be exhaustive, and are made largely for convenience of exposition.

developmental process than to exclude elements from it.[10] Little attention has been paid to setting out the limits of developmental systems, and to individuating one from another. Sterelny has criticized earlier versions of the theory on these grounds: "Elvis Presley is part of my developmental system, being as he was causally relevant to the development of my musical sensibilities, such as they are. Yet surely there is no system, no sequence, no biologically meaningful unit, that includes me and Elvis."[11] The "Elvis Presley" problem helps us clarify the claims of developmental systems theory. The theory aims to provide an explanation of transgenerational stability of form which does not attribute it to the transmission of a blueprint or program in the genome—a pseudo explanation that inhibits work on the real mechanisms of development. So the theory is interested in those developmental resources whose presence in each generation is responsible for the characteristics that are stably replicated in that lineage. For example, we might contrast two influences on a newborn bird. The interaction between the newborn bird and the song of its own species, which occurs in each generation and helps explain how the characteristic song is produced, is part of the bird's developmental process. The interaction between the newborn bird and the noise that ruptures its eardrums plays no such role, and so is not part of the process.

Another way to draw this distinction is by distinguishing developmental outcomes that have evolutionary explanations from those which do not. The interactions that produce outcomes with evolutionary explanations are part of the developmental system. There is an evolutionary explanation of the fact that the authors of this paper have a thumb on each hand. We have thumbs because of the replication of thumbed ancestors. The thumb is an evolved trait. But the fact that one of us has a scar on his left hand has no such explanation. The scar is an individual trait (we are referring, of course, to the trait of having a scar just thus and so, not the general ability to scar). The resources that produced the thumbs are part of the developmental system. Some of those which produced the scar, such as the surgeon's knife, are not.

Various issues need to be clarified about this historical or etiological characterization of the developmental system. First, the distinction between "evolved" and "individual" outcomes is not another version of the innate/acquired distinction. It is not a distinction

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[10] In writing this section, we have been influenced by Ruth G. Millikan's *Language, Thought, and Other Biological Categories* (Cambridge: MIT, 1984). In this area as in many others, Millikan has broken the ground for those interested in biological teleology/teleonomy.

[11] Personal communication.

between types of developmental processes. The fact that a developmental outcome has an evolutionary history is not an intrinsic property that can be determined by inspection of the outcome, or of the process that constructs it. By calling it an evolved outcome we are merely indicating that it fits into a particular pattern of explanation. Similarly, when we privilege certain of the resources that go to construct an organism as "the developmental system" we do so to point to the explanatory connection between the transgenerational stability of these resources and the transgenerational stability of certain developmental outcomes. For other explanatory purposes, such as the study of developmental abnormalities, a different system must be delineated.

The fact that the evolved/individual distinction is not a distinction between different types of developmental process cannot be too much stressed. Past interactions between evolutionary theory and developmental theory have not had happy outcomes. Evolutionary theorists like Lorenz used the category of innateness to substitute an evolutionary explanation for a genuine developmental explanation. We hope that a developmental systems account of evolution can avoid this mistake, because it makes the developmental mechanisms themselves the prime focus of evolutionary explanation.

A second important point of clarification is that the claim that all features of the developmental system can be given evolutionary explanations does not commit us to any form of adaptationism. Evolutionary explanation is "adaptive-historical" explanation. The organism's response to any particular adaptive phase is determined in part by the historical resources and historical constraints accumulated in the lineage in response to past phases. The outcome of the process is affected by these resources and constraints, and they themselves are altered by the outcome of the process. The outcome is also influenced by the availability and order of variants and by the sheer stochasticity of the differential replication process. So even in cases where adaptation plays a role in the explanation of a particular trait, that explanation is very far from adaptationist. Furthermore, the developmental system is not a collection of separately evolved features. The system of interdependences that it represents is itself an evolutionary product. Vestiges and features produced because of developmental correlations are as much evolved features of the developmental system as features that offer some adaptive advantage. They, too, are subject to adaptive-historical explanation.[12]

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[12] The word 'adaptationism' was introduced in Stephen J. Gould and Lewontin, "The Spandrels of San Marco and the Panglossian Paradigm: A Critique of the Adaptationist Programme," *Proceedings of the Royal Society of London,* CCV

IV. DEVELOPMENTAL SYSTEMS AND EXTENDED PHENOTYPES

The idea of a developmental system has certain parallels with Richard Dawkins's[13] notion of the extended phenotype. We believe that Dawkins's central insight was that many elements outside the traditional organism can be given an evolutionary explanation. Nests vary through evolution, and the number and form of current nests has been influenced by the relative effectiveness of these variations.

Dawkins claims that such explanations are possible because of the selection of genes associated with the production of extended phenotypic features, such as nests. But the central insight just described is completely independent of Dawkins's gene-selectionist view of evolution. The phenomena of habitat imprinting demonstrates very nicely how the association of an organism with an environmental feature could have an evolutionary explanation without the genes having an interesting role in the production of that trait. Klaus Immelmann[14] cites a study of European mistle thrushes which clearly illustrates this. The expansion of this species' range from forest to parkland in France and Germany was shown to proceed, not by the spread of several local populations, but by the spread of a single population that had become habitat imprinted on parkland rather than forest. The fate of different thrush lineages will depend on their interaction with the particular habitat with which they are reliably associated, and the fate of that habitat. The habitat is something they have acquired through evolution, as much as any other element of the phenotype. Yet the genetic variation between the two populations can be presumed to be random with respect to which habitat they have imprinted on. No difference in the mechanism in the two lineages is needed to sustain their association with two very different habitats.

We have argued against Dawkins's interpretation of his extended phenotype cases in genic terms, but we do not want to reject the

(1979): 581–98. The idea of adaptive-historical explanation is discussed in Griffiths, "Cladistic Classifications and Functional Explanations," *Philosophy of Science* (forthcoming). For examples of nonadaptationist evolutionary explanation in a developmental systems account, see Gray, "Metaphors and Methods: Behavioral Ecology, Panbiogeography and the Evolving Synthesis," in *Evolutionary Processes and Metaphors,* Ho and S. W. Fox, eds. (New York: Wiley, 1988): 209–42. For an integration of the idea of developmental constraint with evolutionary explanation, see K. C. Smith, "Neo-rationalism versus Neo-Darwinism: Integrating Development and Evolution," *Biology and Philosophy,* VII (1992): 431–52.

   [13] *The Extended Phenotype* (New York: Freeman, 1982).
   [14] "Ecological Significance of Imprinting and Early Learning," *Annual Review of Ecology and Systematics,* VI (1975): 15–37.

cases themselves. We think that there are many valid evolutionary explanations of extragenic developmental resources. The forms of nests, webs, and so forth do change over evolutionary time in a way that can be explained by the differential replication of lineages. In an earlier paper, one of us[15] has drawn attention to the co-evolution of the certain eucalypts and the bushfires that play such a role in their development. Developmental systems theory makes all developmental interactions subject to evolutionary explanation. Any species-typical occurrence that contributes to development has a history, and its continued occurrence has an adaptive-historical explanation. It is because of this feature that we claim that developmental systems theory maximizes the explanatory power of evolution. It allows the formulation in a single theoretical framework of all natural historical narratives that are genuinely explanatory. This is a simple consequence of the way that we have defined the developmental system. It is precisely by having such an explanation that an item gets to be part of the system.

The developmental systems theorist's version of the "extended phenotype" is not subject to the sort of deflationary reinterpretation that Sterelny and Kitcher use to attack Dawkins (*op. cit.*). According to Sterelny and Kitcher, Dawkins's extended phenotypic features can be reduced to traditional behavioral phenotypic features. His talk of genes for webs or nests can be replaced by talk of genes for web or nest building behavior. Thus, while they admit that Dawkins's picture of evolution can be illuminating, they deny that it explains anything that could not be effectively explained already. A traditional evolutionary theory can explain the evolution of the behavior, and simply note the effects of this behavior on the environment.

This deflationary strategy cannot be applied to many of the features that count as part of our "extended phenotype." Developmental systems theory claims to give evolutionary explanations of all the developmental interactions. Among them are those like the thrush case just described, in which the organism interacts with a persistent environmental feature. The interaction may have an evolutionary explanation. It may be that some lineages have survived because they were imprinted on an advantageous habitat. But the interaction cannot be reduced to a feature of the traditional behavioral phenotype. This is clearly shown by another example cited by Immelmann (*op. cit.*). Cuckoo-style parasitic viduine finches have developed morphological subspecies and species on the basis of historic associations with different parasitized species. These associations are

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[15] Gray, "Death of the Gene."

sustained by host imprinting. It is highly plausible that being asso-
ciated with a successful host species, and one that has not developed
antiparasitic adaptations is a critical factor in success for the para-
sitic species. Developmental systems theory can give an evolutionary
explanation of the developmental interaction between parasite lin-
eage A and host lineage B. An account that confines itself to the
traditional behavioral phenotype can only explain the general trait
of host imprinting, which is common to all the species, and then
state that this particular parasitic species has been historically asso-
ciated with this particular host species. It cannot encompass the fact
that association of the particular parasite A with the particular host
B has itself evolved by the differential replication of this and other
associations.

One difficulty arises, however, from our enthusiastic extension of
the phenotype. Genes are a developmental resource, and their dif-
ferential replication depends on the success of the system of which
they are a part. More surprisingly, bushfires are a developmental
resource, and their replication depends in part on the success of the
plants for which they are a resource. But sunlight and gravity are
also developmental resources, and play a critical role in determining
evolved developmental outcomes. Surely, we are not proposing that
features of this kind can be given evolutionary explanations? It is to
this issue that we now turn.

V. WHAT IS REPLICATED IN DEVELOPMENT?

The evolutionary account of the limits of the developmental system
given in section II makes no distinction between developmental re-
sources that owe their existence to the past generations of the devel-
opmental system, and those which exist independently of it. Some
elements of the system are actively replicated by the parent organ-
ism (genes, cytoplasm, language traditions), and some are present
because of the collective activities of the population (libraries, land-
scape features), but some merely persist from generation to genera-
tion (sunlight, gravity, parkland habitats for thrushes). Even if we
have succeeded in showing that many elements of what is tradition-
ally conceived of as the environment have an evolutionary history,
surely we have gone too far by including merely persistent features?
Surely there is no interesting sense in which persistent features are
part of the evolutionary process? Instead, the objection goes, we
should treat them as passive features of the environment, in the
traditional fashion.

We are not impressed by this objection, and think that it over-
looks an important sense in which persistent environmental features
are part of the evolutionary process. Although the sun persists with-
out reference to the evolution of a developmental system, its inter-

action with the rest of the system is highly contingent. A change in other developmental interactants which results in the organism behaving differently may substantially modify its interaction with the sun. If the organism becomes cave-dwelling, the interaction may cease completely. The phenomena of habitat imprinting, in which an organism's choice of environment is a function of an earlier developmental interaction, shows the interaction with "persistent" habitat features being actively replicated. There is a fundamental similarity between building a nest, maintaining one built by an earlier generation, and occupying a habitat in which nests simply occur (for example, as holes in trees). In all three cases, there may be an evolutionary explanation of the interaction of the nest with the rest of the developmental system.

The objection is useful, however, in that it forces us to consider more closely the ontology of developmental systems. We suggest that the primary focus of a constructionist account of development should be on developmental processes, rather than developmental systems. The developmental process is a series of events which initiates new cycles of itself. We conceive of an evolving lineage as a series of cycles of a developmental process, where tokens of the cycle are connected by the fact that one cycle is initiated as a causal consequence of one or more previous cycles, and where small changes are introduced into the characteristic cycle as ancestral cycles initiate descendant cycles. The events which make up the developmental process are developmental interactions—events in which something causally impinges on the current state of the organism in such a way as to assist production of evolved developmental outcomes. The things that interact with the organism in developmental interactions are developmental resources. Some of the resources are products of earlier stages of the process, others are products of earlier cycles of the process, others exist independently of the process. These distinctions, while real, do not bear on the type of role which the entity plays in the developmental process.

The limits of the developmental process are set using the historical scheme of individuation which we applied to developmental systems in section II. An interaction is part of the developmental process if it is of a type that has played a role in the evolution of the process. In the light of this revision, we might define a developmental system as the sum of the objects that participate in the developmental process, or, alternatively, as the sum of the developmental resources. We can now fix the limits of evolutionary explanation a little more precisely. All developmental interactions (as defined above) have evolutionary explanations, and some resources do. The distinction between explaining an interaction and explaining the

resource that interacts is not just an ad hoc distinction invented to get around this problem. In a previous paper, one of us[16] has worried over the fact that object trouvé, such as the shells occupied by hermit crabs, are clearly adaptations of those organisms, but do not owe their existence, either ontogenetically or phylogenetically, to that organism. We can now see that the interaction between the organism and this resource has an evolutionary explanation, while the resource itself has a quite separate explanation as part of the evolutionary history of another lineage of organisms.

VI. INDIVIDUATING DEVELOPMENTAL PROCESSES

The reformulation of developmental systems theory in terms of developmental processes allows us to resolve some outstanding puzzles for the theory. First, it allows us to confront the obvious objection that developmental systems do not form discrete generations, and so cannot provide the ancestor-descendant sequences required for evolution. Sterelny and others have suggested to us that once we lose sight of the sequence of individual genomes, separated from one another by the bottleneck of the zygote, we have no univocal basis for dividing up a "lineage" of developmental systems into discrete generations. It would be all very well if developmental systems theory only extended inheritance to include the nongenetic element of what we have labeled "parental resources." These resources, such as the maternal cytoplasm, cycle in synchrony with the genes. But, in fact, the developmental system includes the persistent resources, such as sunlight, and the population generated resources, such as speech communities. The full range of developmental resources exhibit a bewildering variety of periodicities.

The objection can be put as a dilemma. On the one hand, does the developmental systems theory concede a privileged role to the genes in defining the temporal boundaries of an individual? That seems inconsistent with the whole thrust of the approach. On the other hand, if the theory rejects this privileged role for the genes, what account can it offer of the individuals in a lineage of developmental systems? The view developed in the last section allows us to slip between the horns of this dilemma. The central theoretical entity in our account is the developmental *process,* rather than the developmental *system.* The developmental process is a series of interactions with developmental resources which exhibits a suitably stable recurrence in the lineage. Its periodicity is unrelated to that of the resources themselves.

A simple thought experiment can help to clarify how the move to developmental processes helps with the present objection. Imagine

[16] Griffiths, "Functional Analysis and Proper Function," *British Journal for Philosophy of Science,* XLIV (1993): 409–22.

a lineage of asexuals in which each individual succeeds in begetting only a single viable offspring, and in which the individual dies with the birth of this offspring. What we have is a continuous series of developmental interactions. The problem is to find some way of chopping it up into generations (or individuals). Our proposal is to look for a particular sequence of interactions which is substantially repeated throughout the lineage. One repetition of this sequence of interactions constitutes a generation. Each repetition is an individual.

It is now possible to introduce some complications. First, suppose that the previous generation does not die at the inception of the next, and that an individual can give rise to more than one offspring, and to more than one batch of offspring. In that case, the lineage has a more complex topology, an irregular bush rather than a straight line, but the same empirical investigation can be carried out. Its aim might now be more clearly expressed as finding an atomic unit of which this topology is composed. In a further complication, we can suppose that reproduction is sexual. The topology of the lineage becomes reticulate, but there seems no additional obstacle to the search for an atomic unit, which might be more intuitively described as a *life cycle*. This may help to prevent confusions engendered by taking 'developmental process' to refer to development to adulthood.

It might be asked why we are so confident that the series of developmental interactions will have this cyclical structure. In reply, we are able to take over a well-known argument. The evolution of complex, functional structures requires a repeated life cycle during which structures are repeatedly reassembled. In Dawkins's version of this argument, he contrasts an organism that grows ever larger, with variations in its constituent cells merely giving it a mosaic structure, with one that grows to a finite size, and then begets descendants (*op. cit.*, pp. 256–64). Only in the later case do variations have the opportunity to create a major reorganization of the overall structure of the organism, or of any of its complex subsystems. Thus, we can expect complex, functional systems to be produced by the repetition with variation of a developmental sequence. Dawkins construes this argument as providing support for the central importance of the Weissmanian bottleneck in evolution. He moves from the argument just outlined to a definition of an individual as a segment of a lineage isolated at each end by a single-cell bottleneck. But this genophilic conception is not supported by the argument. What the argument actually supports is the view that the evolution of functional complexity will be favored by the repeated reconstruction of the functional structures. This is entirely compatible with our

view of development, in which these structures are produced by a
developmental process/life cycle that draws on a wide range of in-
herited resources. On the developmental systems view, what sepa-
rates individuals is not the existence of a developmental bottleneck,
but the fact that substantially similar functional structures are re-
constructed anew from the developmental resources. We therefore
help ourselves to the argument to explain our confidence that lin-
eages of developmental processes/life cycles will exhibit the repeti-
tive structure that we require.

We have tried to show that lineages will exhibit enough cyclical
structure to support our proposal for individuating developmental
systems. The next problem is that lineages may contain too much
cyclical structure. In many lineages, larger developmental cycles ex-
ist that embed several traditional phenotypic life cycles. We may be
faced, therefore, with an embarrassment of riches as regards re-
peated sequences of developmental events. In aphids, for example,
the cycle of birth and death of traditional phenotypic individuals is
nested within a larger seasonal cycle. A cycle of sexual reproduction
is followed by a series of asexual reproductive cycles, terminated by
a further sexual phase. D. H. Janzen[17] and others have suggested
that the whole asexual clone be regarded as the genuine "evolution-
ary individual." In our terms, this amounts to the suggestion that
the development of individual aphids in the asexual phase be re-
garded as repeated components of a developmental process, like the
development of individual leaves on a single plant. Clearly, we need
to place extra conditions on the sorts of repeated developmental
processes that constitute an "evolutionary individual," as opposed
to an iterated sequence in the development of an individual.

As a first step, we can make use of the evolutionary rationale that
we have suggested for the cyclical nature of developmental pro-
cesses. This leads us to reject the suggestion that the developmental
process that produces an individual aphid is not in itself a life cycle
in our sense. Variations in the resources that feed into the asexual
production of an individual aphid can restructure this process in
ways that are reflected in descendant processes. This process is
therefore a life cycle of the sort that forms evolving lineages. This is
not to suggest, of course, that the longer cycle is not also an evolu-
tionary life cycle. Like many other accounts of evolution, the devel-
opmental systems view allows evolutionary units to embed one
another. The key to identifying a new unit of self-replication will be
to find new events and entities whose numbers, proportions, and

    [17] "What Are Dandelions and Aphids?" *American Naturalist*, CXI (1977):
586–9.

properties can be explained as the result of the differential replication of the larger life cycles in which they are involved. Developmental systems accounts of intragenomic evolution, as in the evolution of meiotic drive mechanisms, could be constructed. Developmental systems accounts of group selection are also possible.

The developmental systems position on the unit of selection debate is thus a form of pluralism. There may be several "levels" of life cycles, accounting for different features of evolved systems. We are suspicious of the term 'level' here, however, since investigation has not yet proceeded far enough to determine to what extent processes at one "level" can be considered independent of those at other "levels." There is also no real basis for making "horizontal comparisons" among processes, so as to give a definite meaning to the statement that two processes are at the "same level." More investigation of these topics is clearly called for.

It might appear that this interpretation of the aphid case commits us to the view that, for example, metamorphosis in insects constitutes the end of one life cycle and the beginning of another.[18] Variation in a developmental resource at this point certainly has the potential to cause major heritable alterations to the life cycle. This conclusion does not follow, however, as can be seen by considering the modified life cycle that would result from such a variation. Variation in a developmental resource that caused a different outcome to metamorphosis would give rise to a variant life cycle that recapitulated the phase before the metamorphosis. It would thus be a variant on the larger life cycle of which the metamorphosis is a phase, not a variant in a life cycle with the metamorphosis as its beginning. Hence metamorphosis is a stage in a single life cycle, not the end of one and the beginning of another.[19] Similar considerations explain why the growth of a leaf is an iterated component of a plant's life cycle, not a life cycle in itself. The descendants of variant leaves, if they have any, are variant plants.

A final clarification of our view can be obtained by considering the standard question of the status of vegetative clones. Consider a rhododendron bush that develops where the branch of another bush touches the ground. For Dawkins, its claim to be a new evolutionary individual is fatally undermined by its failure to pass through

[18] Dawkins's discussion of this case is interestingly unresolved. He would presumably avoid the idea that metamorphic stages are individuals by pointing to the absence of a single-celled bottleneck.

[19] If the effect of a variation at metamorphosis was not as we have envisaged it, and the modified organism gave rise to descendants that bypassed the phases before the metamorphosis, we would have to say that what was previously a phase of a developmental process was now a developmental process in its own right. But in this extraordinary case that would be the right thing to say.

a single-cell bottleneck. In his view, any organism that reproduces in this way, via a multicellular propagule, must eventually see its functional organization break down because of the divergent genetic interests of the various cell lineages of which it is composed. We reject this conclusion because the single-cell bottleneck is only one way of making a complex system function as a single evolutionary unit. Leo Buss,[20] for example, has drawn attention to the role of the rigidity of plant cell walls, and consequent restrictions on movement, in restricting the potential for conflict between cell lines and allowing the retention of vegetative reproduction as a major mode of propagation. On our view, the individual rhododendrons may well be genuine individuals. The growth of the plant from the initial rooted branch involves the reconstruction of its functional structures from a range of developmental resources, and gives ample opportunities for the development of variant forms as the result of alterations in one or more of those resources.

In summary, we claim that the individual, from a developmental systems perspective, is a process—the life cycle. It is a series of developmental events which forms an atomic unit of repetition in a lineage. Each life cycle is initiated by a period in which the functional structures characteristic of the lineage must be reconstructed from relatively simple resources. At this point there must be potential for variations in the developmental resources to restructure the life cycle in a way that is reflected in descendant cycles.

VII. TYPE AND TOKEN IN DEVELOPMENTAL PROCESSES

In reply to our treatment of vegetative reproduction in the last section, it might be objected that vegetative reproduction omits certain of the early stages of development seen in sexual reproduction in the same lineage, and so is not a repetition of the same developmental process. This objection picks up on the important fact that life cycles may have a disjunctive form, with different individuals having different characteristics. A developmental system can proliferate by producing a range of outcomes on different occasions. This accounts for much of the graded individual variation between organisms. Different humans develop a range of heights. In some circumstances one height is advantageous, in others a different height. The system that is replicated as a result of these individual successes and failures is one that produces a range of heights. All heights in the range are evolved outcomes.

A very similar conceptualization will allow developmental systems theory to encompass the idea of "alternative life-history strategies." The successful developmental systems in certain beetle lineages have been those which produce one outcome in response to one sort of

[20] *The Evolution of Individuality* (Princeton: University Press, 1987).

interaction, and another in response to a different interaction. The first produces a large, well-armed morph, the second a smaller morph that avoids conflict. Morphs of one type regularly give rise to the other morph. Both morphs are expressions of the same developmental system. The two life cycles of individual rhododendrons, sexual or asexual, are alternative life-history strategies. This is perhaps obscured by the fact that they converge over time, rather than diverging, as in more stereotypical cases. Life cycles of one type regularly give rise to life cycles of the other, so both are segments of the same lineage.

We have shown that very different token developmental processes may be of the same type. This fact also allows us to capture Lorenz's insight that many of what we have termed "individual traits"—those lacking an evolutionary explanation, may be seen as evolved traits, with full evolutionary explanations, if typed under a more general classification scheme. As Lorenz made famous, it is an evolved developmental outcome in certain waterfowl that they imprint on the first suitable object they see. So the thing they interact with is part of their developmental system. But it is not an evolved developmental outcome for them to imprint on any particular individual, like Lorenz's greylag goose Martina. Although Martina is part of her offspring's developmental system, it would be misleading to describe the situation this way. The general point here is that resources are parts of developmental systems because of generalizations about their role in producing evolved outcomes. In describing the system, we should use descriptions with sufficient generality to enter into these generalizations. There are evolutionary generalizations about the importance of imprinting on parents, and of imprinting on the first largish moving thing, but not one about the importance of imprinting on Martina, or on Lorenz.

This account of how to type-classify elements of the developmental system is the key to how the theory handles learning, and other cases where Lorenz would have invoked the interplay of "ontogenetic information" and "phylogenetic information." Electric light sockets have as yet played little role in human evolutionary history, yet my fear of them has an evolutionary explanation.[21] The key lies in choosing the right description. Fear of objects associated with injury, or with fear displays in conspecifics is an evolved developmental outcome. There are evolutionary explanations of my acquiring a fear of any such object. So the resources that produce an organism with such fears are parts of the developmental system. My

[21] See Griffiths, "Modularity and the Psychoevolutionary Theory of Emotion," *Biology and Philosophy*, II (1990): 175–96.

trait of being afraid of light sockets is an evolved developmental
outcome, but only under a general description of the form: 'being
afraid of objects with such and such a role in my past learning
history'. The light sockets are part of my developmental system, but
only under the general description of objects that play that role.

These considerations allow us to describe adequately the case of
Sterelny and Elvis Presley raised in section III. Perhaps there is an
explanation of the ability to conform to the preferences of whatever
group we find ourselves in at a certain age. In that case, Elvis is part
of Sterelny's developmental system, but only under the description
'the preferred object of local aesthetic preference'. But perhaps the
lineages that prefer Elvis are on a separate evolutionary trajectory!
If an Elvis-filled upbringing makes its recipients likely to prefer
Elvis, and if this preference makes them unlikely to achieve success-
ful mating with anyone not similarly inclined, we have the potential
for speciation! The ability of the developmental systems approach to
explain relationships to individual objects, as well as to types of
objects, comes to the fore here. In the extreme version of the Elvis
case, there would be a lineage for whom Elvis was part of their
developmental system, just as the scent of the home river is part of
the developmental system of a lineage of salmon. The relationship
between the individual lineage and this particular object is a key part
of the evolutionary history of the lineage.

VIII. WHAT IS REPLICATED IN EVOLUTION?

Current mainstream accounts of evolution distinguish two sorts of
entities that play distinct roles in the evolutionary process—replica-
tors and interactors. The prototype replicators are genes. According
to Dawkins,[22] the genes replicate themselves and exhibit continuity
over the generations. They exhibit "longevity, fecundity, and fidel-
ity" and are potentially "immortal" (*ibid.*, pp. 37–8). Other features
of the organism are mere devices of the genes, whose role is to
interact with the environment in the genes' interests. These pheno-
typic and extended phenotypic features he calls "vehicles" (Hull[23]
has replaced Dawkins's loaded term 'vehicle' with the term 'interac-
tor'). Pace Dawkins, we believe that the replicator/interactor dis-
tinction is not driven by considerations of evolutionary theory. It is
the projection into evolution of the dichotomous views of develop-
ment that we have criticized above. A developmental systems ac-
count of evolution has no use for the replicator/interactor
distinction.

[22] *The Selfish Gene* (New York: Oxford, 1976).
[23] *Science as a Process* (Chicago: University Press, 1988).

Dawkins has tried to insulate his gene-selectionist view of evolution from views about the role of the genes in development. He argues that "when we are talking about development it is appropriate to emphasise nongenetic as well as genetic factors. But when we are talking about units of selection a different emphasis is called for, an emphasis on the properties of replicators."[24] But the two issues cannot be kept apart in this way, because the claim that only genes are replicators is based on an analysis of their role in development. To quote Dawkins himself: "The special status of genetic factors is deserved for one reason only: genetic factors replicate themselves, blemishes and all, but non-genetic factors do not" (*ibid.*, p. 99).

But what exactly is it that has the power to replicate itself? A segment of DNA isolated from the cytoplasmic machinery of ribosomes and proteins has no such power. Suppose we enumerate the whole cellular machinery needed to copy a strand of DNA, including the independently inherited centrioles, mitochondria, etc. This is very far from Dawkins's original vision of the immortal gene. Furthermore, under natural conditions this system only replicates itself because of the presence of all the other developmental resources. As Richard Lewontin[25] has remarked, "if anything in the world can be said to be self-replicating, it is not the gene, but the entire organism as a complex system" (*ibid.*, p. 48).

Once again, the supposed asymmetry between the role of the genes and the role of other developmental resources evaporates when closely analyzed. The genes replicate themselves by making a contribution to a developmental process that can initiate new cycles of itself. Other developmental resources do just the same. In one of the earliest responses to Dawkins, Bateson[26] observed that, if we say a nest is a gene's way of making another gene, we may as well say that a gene is a nest's way of making another nest. The rhetoric of "self-replicating" genes, while no doubt always intended as an ellipsis for replication in a broader organismic context, has distracted attention from this symmetry between the replication of genes and the replication of many other developmental resources.

According to developmental systems theory, all developmental interactions are replicated, as part of the replication of the develop-

[24] *The Extended Phenotype*, p. 98.
[25] *Biology as Ideology: The Doctrine of DNA* (New York: Harper Collins, 1993). For an extended critique of the replicator/interactor distinction, see J. R. Greismer, "The Informational Gene and the Substantial Body: On the Generalisation of Evolutionary Theory by Abstraction," in *Varieties of Idealisation*, N. Cartwright and M. Jones, eds. (Amsterdam: Rodopi, 1982).
[26] "Review of R. Dawkins's *The Selfish Gene*," *Animal Behaviour*, LXXVIII (1978): 316–8.

mental process/life cycle. Many of the elements of the developmental system—the developmental resources—are also replicated, as a consequence of the process. Some of these serve as resources for later stages of the process, others as resources for future generations. If we insist that a replicator have the intrinsic causal power to replicate itself, there will be only one replicator, the life cycle. But if we allow the status of "replicator" to anything that is reliably replicated in development, there will be many replicators. In the terminology of figure 1, the replication of developmental processes or life cycles (D) gives rise to the replication of all the developmental interactions that make up the process (represented by the arrows in figure 1) and of all the developmental resources that are not merely persistent (B, C, E). The theory of evolution is the theory of the change over time of the numbers, proportions, and properties of all these things.

IX. SELECTION AND COMPETITION IN DEVELOPMENTAL PROCESS EVOLUTION

Taking developmental processes, rather than genes or traditional phenotypes, to be the units of evolution requires a substantial reformulation of evolutionary theory. Yet the fundamental pattern of explanation—the development of complex form through variation and differential replication—is preserved. Perhaps the most radical departure is that the separation of organism and environment is called into question.[27] Evolution occurs because there are variations during the replication of life cycles, and some variations are more successful than others. Traditionally, variants are said to be exposed to independently existing selective forces, expressions of an independently existing environment. In the developmental systems representation, the variants differ in their capacity to replicate themselves. One variant does better than another, not because of a correspondence between it and some preexisting environmental feature, but because the life cycle that includes interaction with that feature has a greater capacity to replicate itself than the life cycle that lacks that interaction. This perspective is appropriate, because many of the features of the traditional environment have evolutionary explanations. Organism and environment are both evolving as an effect of the evolution of differentially self-replicating life cycles. Life cycles still have fitness values, but these are interpreted, not as a measure of correspondence between the organism and its environment but

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[27] The dissolution of the organism/environment distinction has been urged by other proponents of the developmental systems perspective. See Lewontin, "The Organism as the Subject and Object of Evolution"; Oyama, "Stasis, Development and Heredity," in *Evolutionary Processes and Metaphors*.

as measures of the self-replicating power of the system. Fitness is no longer a matter of "fittedness" to an independent environment.

Our reinterpretation of natural selection as differential replication draws attention to a frequently neglected class of evolutionary events. There are many variations in developmental processes which are hard to interpret as improvements in the organisms fit to pre-existing selective forces. The cases of birds varying and differentially reproducing in virtue of different habitat associations (discussed in section IV) provide one example. Another would be cases in which the organism's activity modifies its environment, as when a change in the habits of a eucalypt increases the probability of bush fires. These cases are more easily understood as the incorporation into the developmental process of elements that increase its self-replicating power.

One traditional notion that remains very little changed is that of competition. Competition occurs when two or more developmental processes utilize the same resources, and there is a limit to these resources. This may occur because persistent features in the environment are developmental resources for both systems, as when members of different lineages occupy the same limited number of nest sites. It may also occur because resources produced by one process are utilized by another in a way that denies them to future cycles of the first process. Brood parasitism in birds and insects is one example. So competition occurs when a single developmental resource is part of more than one developmental system. Not all interpenetration of developmental systems constitutes competition, however. Mutualisms are a positive form of interpenetration, and there are also neutral forms, such as hermit crabs occupying discarded whelk shells.

X. IMPLICATIONS FOR "CULTURAL EVOLUTION"

The developmental process view changes the relationship between biological and cultural evolution. This distinction rests on a distinction between genetically transmitted and environmentally acquired traits. For example, Elliott Sober[28] defines cultural evolution as the process in which traits are passed on by learning, rather than by the transmission of genes, and where fitness is measured by how many people learn them, not by how many copies of genes are passed on. Current discussions of evolution often give the impression that cultural evolution began when biological evolution left off! Humans, it is suggested, derived a set of "biologically based" characters before

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[28] "Models of Cultural Evolution," in *Trees of Life: Essays in Philosophy of Biology*, Griffiths, ed. (Boston: Kluwer, 1992).

and during a pleistocene hunter-gatherer phase.[29] These traits are genetically based, and have been passed down largely unchanged. During this period, however, they acquired an enhanced capacity for learning and for the transmission of information. Cultural structures began to be passed down which are not genetically based. Most change since that period is the result of this latter process.

The developmental systems view implies that it is not possible to divide the traits of organisms into those with a genetic base, which can be explained by biological evolution, and those which are environmentally acquired and are the domain of cultural evolution. The means by which traits are reconstructed in the next generation are varied, and do not admit of any simple twofold division of the sort just described. Instead, all traits that are typical of a lineage are subject to a form of evolutionary explanation that describes how developmental processes replicate and differentiate into lineages as part of an adaptive-historical process. Many elements of the developmental systems associated with these processes can be given evolutionary explanations. Some of these will be elements of the traditional organisms, such as genes. Others will be elements of culture, such as the social structures that are required for the replication of evolved psychological traits in humans.

The developmental systems view emphasizes the currently marginalized fact that humans have had a culture since before they were human. This culture is one of the developmental resources that feeds into the development of evolved traits. It has a history of development and differentiation among lineages as old as that of many other elements in the developmental system. Many species-typical features of human psychology may depend critically on stably replicated features of human culture. Many psychological features that are specific to certain human cultures may nevertheless have evolutionary explanations, since this variation may reflect differentiation among lineages of developmental systems. An obvious research program within developmental systems theory is an attempt to locate critical developmental resources in human culture(s), and to study their influence on development, and how they themselves are replicated.

Two objections are commonly urged to the idea that cultural evolution can be accommodated in the same theoretical framework as the evolution of traditional biological traits. First, it is often remarked that culture changes much more rapidly that any biological trait. But how rapidly something changes depends on how it is taxonomized. The forms of relationship between the sexes in European

[29] This view is clearly dominant in an important recent collection of papers on human evolution: The Adapted Mind, J. H. Barkow, L. Cosmides, and J. Tooby, eds. (New York: Oxford, 1992).

society has changed greatly in the last thousand years, but it has remained fundamentally patriarchal. Developmental systems theory suggests an attempt to locate the fundamental developmental resources that account for the stability of this feature. These will be classified in such a way as to allow them to be identified across the whole range of such societies. The second common objection to evolutionary approaches to culture is that cultural traits are transmitted horizontally, rather than vertically, and that this gives cultural evolution a fundamentally different structure from biological evolution, in which traits are transmitted vertically. In such a process, it is suggested, the idea of lineages as the fundamental units of evolution is inappropriate. One response to problems of this kind would be to enlarge the size of the lineage groups studied so as to reduce the incidence of such transmission between the units of study.[30] But this may not be necessary, as the traditional contrast between cultural and biological is overdrawn on both sides. On the biological side, plant evolution and bacterial evolution involve a good deal of horizontal transmission (via hybridization and plasmid exchange). This calls for some revision of traditional methods in studying bacterial evolution, but not enough to render them unrecognizable.[31] On the cultural side, it is plausible that transmission is "vertical" to a remarkable extent. Languages exchange items of vocabulary, but do not merge wholesale. This form of horizontal transmission is closely akin to plasmid exchange. Some studies have claimed a substantial parallelism between trees for language and genetic trees for human lineages.[32] All elements of these comparisons are currently poorly empirically based, and should not be relied upon, but it is not inconceivable that Dr. Johnson spoke truer than he knew when he said that "languages are the pedigrees of nations."

XI. CONCLUSION

The developmental systems tradition in biology reflects a continued dissatisfaction among many workers with conventional, gene-centered accounts of development and evolution. Several authors have tried to replace this dichotomy with the idea of a developmen-

[30] See R.J. O'Hara, "Evolutionary History and the Species Problem," *American Zoologist* (forthcoming).

[31] For the implications of bacterial plasmid exchange for taxonomy, see J. Maynard-Smith, "The Evolution of Prokaryotes: Does Sex Matter?" *Annual Review of Ecology and Systematics*, XXI (1990): 1–12. For implications of hybridization in plants, see L. McDade, "Hybrids and Phylogenetic Systematics I. Patterns of Character Expression in Hybrids and their Implications for Cladistic Analysis," *Evolution*, XLIV (1990): 1685–700; "Hybrids and Phylogenetic Systematics II. The Impact of Hybrids on Cladistic Analysis," *Evolution*, XLVI (1992): 1329–46.

[32] L. L. Cavalli-Sforza *et al.*, "Reconstruction of Human Evolution: Bringing Together Genetic, Archeological and Linguistic Data," *Proceedings of the National Academy of Sciences*, LXXXV (1988): 6002–6. D. Penny, E. E. Watson, and M. A. Steel, "Trees from Languages and Genes Are Very Similar," *Systematic Zoology*, XLII (1993): 382–4.

tal system. Our main aim in this paper has been to make this idea precise. We have shown how to define the system in terms of a developmental process. The developmental process or life cycle is a series of developmental events which forms a unit of repetition in a lineage. Each life cycle is initiated by a period in which the functional structures characteristic of the lineage must be reconstructed from relatively simple resources. At this point there must be potential for variations in the developmental resources to restructure the life cycle in a way that is reflected in descendant cycles. The developmental system is the structured set of resources from which the life cycle is reconstructed in each generation.

Developmental systems theory offers to free biology and the social sciences from the grip of dichotomous accounts of development. Traits need not be either genetic or environmental, either evolved or socially constructed. While there has been a general agreement that these dichotomies are mistaken, attempts to replace them have generally reproduced the same problem in a subtler form. For example, the insistence that all traits depend on both genic and nongenic factors is followed by an attempt to separate the contribution of the two and evaluate which is the more important in a particular case.[33] To take another case, the admission that a trait covaries with changes in the environment is explained by postulating several genetic programs with environmental "triggers" to choose among them.

We have also sketched the implications of developmental systems theory for the study of evolution. We argued that the prime unit of evolution (unit of self-replication) is the developmental process, or life cycle. Many developmental resources interact with this process, and these have very different characters, ranging from the genes to persistent features of the environment, such as sunlight. But the interaction of all these features is subject to evolutionary explanation. Furthermore, when a feature is replicated, it is due to the replication of the whole process for which it is a resource. Conceiving evolution as the differential replication of developmental processes/life cycles therefore gives us maximum explanatory power, allowing us to explain everything that can be explained in terms of differential replication. As the last section has shown, this scope may be remarkable.

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[33] For a critique of this attempt, see Lewontin, "The Analysis of Variance and the Analysis of Causes," *American Journal of Human Genetics*, XXVI (1974): 400–11.