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Development, Evolution, and Adaptation

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In this paper I develop three conceptions of the relationship between evolutionary and developmental biology. I further argue that: (a) the choice between them largely turns on as yet unresolved empirical considerations; (b) none of these conceptions demand a fundamental conceptual reevaluation of evolutionary biology; and (c) while developmental systems theorists have constructed an important and innovative alternative to the standard view of the genotype/phenotype relations, in considering the general issue of the relationship between evolutionary and developmental biology, we can remain neutral on this debate.

1. Introduction. For over a century, the relationship between developmental and evolutionary biology has been both shifting and uncertain. In the second half of the nineteenth century, the relationship was, if anything, too intimate. Evolutionary biology was dominated by developmental metaphors (Bowler 1988). Orthogenetic conceptions of evolutionary trajectories dominated Darwinian ones. In turn, the program of developmental biology focused on reconstructing phylogeny through recapitulationist principles. However, early in the twentieth century, developmental biology substituted a mechanical agenda for its phylogenetic one and the two biological disciplines went their separate ways. Once developmental biology had acquired its new program, the two fields had very different focal points. Evolutionary biology is a historical science; its central topic is the expansion in space and time of a unique process, the growth of the tree of life. In contrast, developmental biologists study a phenomenon that

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reoccurs regularly in nature. Development is predicable; it may even be programmed. Evolution is neither.

At the same time that developmental biology went proximal, evolutionary theory sloughed off its developmental attachments. Transmission genetics abstracted away from developmental mechanism. Genes were identified through phenotypic variation revealed by crossbreeding. While there was certainly an interest in the physical mechanisms underpinning these variations, the focus of that interest was on the structure, behavior and composition of structures in cells, initially chromosomes. These structures could be investigated without understanding how hybrids developed their novel phenotype. Equally, the identification of alleles through crossbreeding experiments turned only on phenotypes and their frequencies, not on phenotype development. Population genetics had even less connection with developmental biology. Botany, zoology, palaeobiology, systematics, and genetics were explicitly and self-consciously integrated within the single framework of population genetics. The same was not true of developmental biology.¹

So for a sizeable chunk of the century and despite increasing concerns about the disjunction, the two fields developed largely independently of one another. This somewhat equivocal relationship between developmental biology and evolutionary theory persists into contemporary thought. On the one hand, discussion of evolutionary patterns and evolutionary trends still tends to focus on the form of adult organisms. For example, in the discussions of complexity, disparity, and stasis, the critical properties are defined with respect to the form of adult organisms.² Parasites are regarded as simplified by comparison to nonparasitic relatives despite their elaborate life histories. It is typical to talk of a population's environment, niche, and fitness landscape, taking these to be defined by the ecological parameters of the adult organism. Yet there has been at the same time a lively debate about the nature and importance of "developmental constraints" on evolutionary trajectories in general and adaptation in particular (Amundson 1994).

One contemporary line of thought within evolutionary theory suggests that this equivocal status of development within evolution is no accident. Developmental Systems Theorists suggest that developmental biology cannot be integrated within evolutionary biology without a profound rethinking of evolution³. Despite important reservations, I think there is a

1. That is not to say that there were no attempts. De Beer's *Embryos and Ancestors* (1958) is often given an honorable mention in this context.

2. See, e.g., Gould 1989, 1996; McShea 1996; Conway Morris 1998. These works all discuss complexity or disparity in the context of the morphology of adult organisms.

3. The work I principally have in mind is Oyama 1985, Gray 1992, Griffiths and Gray

lot that is right about their view of development (Sterelny et al. 1996). However, in my view the distinctive views of Developmental Systems Theory on development do not bear significantly on the relationship between developmental and evolutionary biology. I doubt that the theory of evolution can be screened off from that of development, but in connecting the two fields we can remain neutral on the distinctive claims of Developmental Systems Theory.

These theorists vary amongst themselves, but on my reading they defend three core claims about development. (1) Though development is predictable, it is not programmed. There is no advantage in seeing the genome as a code or program that specifies the adult organism. (2) Development does not segment into two separate causal streams, one largely driven by the internal resources (especially the genes) of the developing embryo, and the other by environmental resources. Specific developmental outcomes typically depend on resources of both types. So for the purposes of developmental biology the organism/environment boundary is not of critical importance. (3) The developmental cycle from generation to generation is of great significance. But it is usually misleading to conceive of this cycle as initiated solely by the genetic information residing in a single-celled propagule. The bridge of information across the generations is broader and more diverse than that model suggests.

I shall argue that in sensitizing evolutionary biology to developmental information, we can remain neutral on these claims. There is a fourth idea associated with DST which, if accepted, would pose more of a problem for what follows. DST tends to emphasize (especially when rehearsing its skepticism about the idea of innate characters) the interconnectedness and context-sensitivity of development. I will explore some reasons for skepticism about developmental integration at the end of Section 4.

My line in this paper is to sketch three conceptions of a developmental evolutionary biology. In the first two of these, the evolutionary biology that emerges is a very recognizable version of standard contemporary neo-Darwinism. No very revolutionary shift is needed to incorporate developmental insights into an evolutionary perspective. The third is more radical and more controversial. If it were accepted, it would expand and to some degree transform the agenda of adaptationist evolutionary biology. But even here we would be in fairly familiar territory. On one of the views I sketch, development really is not of very great importance for evolutionary biology. If this view is wrong (and two of the three lines of thought

1994. This work draws on an important tradition in developmental and behavioral biology, work typified by Lehrman 1970; Johnston 1987; Bateson 1983, 1991. Jablonka and Lamb 1995 defends some similar ideas on the role of nongenetic inheritance mechanisms.

I consider suggest so), it is wrong because it underplays the significance of the shift from a microevolutionary perspective to a macroevolutionary one. Microevolutionary phenomena—say, the reevolution of a uniform tabbiness in feral domestic cats—can treat both the phenotypic variation available to a population and the environment in which change takes place as fixed. That simplifying assumption becomes questionable as the scale changes. As the temporal scale increases, the issue of available variation becomes central, and that is a phenomenon to which developmental biology speaks. It is often true in science that effects that are negligible at one scale cease to be so when the scale changes; I see the importance of development as an illustration of this theme. The founders of the synthesis were fundamentally concerned with microevolution, and this—together, perhaps, with a too strict interpretation of the idea that macroevolution is microevolution repeatedly re-summed—enabled them to bracket off development.

In the next section I will explore some options for integrating development considerations into evolutionary biology. I will begin with two well-rehearsed issues—developmental constraints and evolutionary novelty—before turning to less usual ideas. One concerns a shift in what we might take to be evolutionary biology's central explanatory agenda. The other takes a skeptical look at developmental entrenchment. In turn, entrenchment leads us to a hypothesis I want to explore in a little more detail, Wagner's "building block" hypothesis.

2. Developmental Evolutionary Biology: Two Mainstream Views. As Rudolf Raff notes, *prima facie*, centaurs would be especially well-adapted. They combine the locomotive adaptations of the quadruped with the manipulative abilities of the biped (Raff 1996, 295). So why do they not exist? Selection depends on the variation available in a population. In the short run, we can usually regard the actual variation in a trait in a population as a good index of the inherent variability of that trait.⁴ But over longer time frames, the variability of traits itself evolves. The nature and spread of heritable variation in an evolving lineage is one key factor in explaining the evolutionary trajectory of that lineage. One version of adaptationism sees evolutionary change as explained externally. On this picture, the environment imposes a set of adaptive demands on a population, and selection shapes that population so that it meets those demands increasingly

4. Though obviously even here caution is called for. Since development and hence variation depends complexly on many factors, it may be that a trait that is currently invariant could show heritable variation in different environments. Relax water stress, for example, and a population of plants might show quite marked differences in growth rate that are masked in an adverse environment.

well (Godfrey-Smith 1996). On this view the role of variation is acknowledged, but there is a tacit assumption that the mechanisms that generate variation will not bias or block evolutionary response to selective pressure. We do not think of oxygen in the air as the explanation of any particular fire, even though it is a necessary condition of combustion. So too in this adaptationist perspective, phenotypic variability is not the cause of a particular adaptive shift, even though it is a necessary condition of any evolutionary change. Rather, those mechanisms are analogous to invariant background conditions like that of oxygen. If the mechanisms that produce variation produce it fairly evenly around the current phenotype of the population, and would continue to do so however that phenotype shifted, it would be reasonable to treat variation as a background condition. Thus if the mechanisms that produce variation (in a given lineage) are decoupled from the realized phenotype (in that lineage) evolutionary biology can bracket off developmental biology. Let us call this the *independence hypothesis*.

The developmental constraints literature involves a guiding assumption that this model of the even spread of variation is in some important way wrong. There is a helpful way of picturing this variation, one introduced in a different context by S. J. Gould. He uses the concept of *morphospace* to depict the variety of life at a time.⁵ That space is the space of all possible organic organizations. For example, the space of all possible shell designs can be approximated in a space of three dimensions: the expansion rate of the shell in the horizontal dimension, the diameter of the spiral, and the rate at which it gains height.⁶ Actual shells occupy only a fraction of this space of possible shells. In general, the variation within a lineage is the volume of morphospace it occupies.

Developmental constraints typically are interpreted as persistent constraints on the phenotypic variability of lineages, constraints which make it difficult or impossible to reach certain regions of morphospace. All mammals have seven neck vertebrae, whereas birds, for example, vary considerably in this respect. This suggests that there may be developmental constraints on vertebrae number in the mammalian lineage. If so, over evolutionary time that lineage will have differential access to the morphospace that surrounds it. If there are developmental constraints on the number but not the thickness of neck vertebrae, then the giraffe design

5. "Morphospace" is not an ideal term, for evolution builds the physiology and behavior of an organism too. Dennett uses "design space" but this term suggests that every aspect of an organism is an adaptation. "Phenotype space" would be a more accurate term, but I have avoided the expansion of terminology.

6. The original work is by David Raup, but it is presented most accessibly in Dawkins 1996.

with extra vertebrae was less accessible to the population of proto-giraffes than the giraffe with thicker vertebrae, and this fact partly explains giraffe phenotypes. If there are developmental constraints in this sense, some biological machines that would work well if they could be built will not be built. Perhaps six-limbed vertebrates cannot evolve, either because no such variants are developmentally possible or because they would have to pass through a developmental fitness valley. Prototype six-legged vertebrates might be very much less well adapted than the four-limbed versions. So we should distinguish developmental constraints narrowly understood, constraints which prevent certain variations *ever arising* in a lineage, and a broader reading of developmental constraints in which development imposes a fitness valley between the current phenotypes in a lineage and some region of morphospace. In the second case, selection is playing a role, but it is not one that depends on specific features of the lineage's environment. Catastrophic developmental failures that happen to be six-limbed are edited out of the population by selection. But selection here does not depend on specific features of the fitness landscape.⁷

A view of evolution that took into account biases in available variation would shift our perspective to a more interactionist conception of evolution, one taking into account both the role of the environment and the role of features internal to a lineage. This is not a very radical change in evolutionary biology. Externalist adaptationism is not received wisdom but is one end point in a spectrum of contemporary evolutionary thought. Many of those who think selection the central force of evolutionary change accept that selective demands are often generated within the lineage itself. Sexual selection, frequency-dependent selection, and social evolution are all selection processes, but not ones in which the lineage is being shaped to an external environment. Moreover, it is often accepted that the environment is not an invariant and unchanging framework to which a population adapts; to the contrary, evolving populations often transform their own environment.⁸ So there are reasons independent of development for questioning externalism.

If the developmental constraints literature is right, development introduces certain biases into the direction of future evolution in a lineage. But it may also help explain the evolution of phenotypic novelty. If the organization of development makes some regions of morphospace hard to enter, it also makes others relatively more accessible. One idea is that

7. Amundson (forthcoming) and Raff (1996, Ch. 9) draw this distinction, though it is often neglected.

8. Lewontin has been particularly important in making this point; see Lewontin 1982, 1985. This line of thought is discussed in Godfrey-Smith 1996, Ch. 5, and Sterelny and Griffiths 1999, Ch. 11.

phenotypic novelty often results from changes in both the absolute and relative timing of development. On this picture, though development begins with a single point and process, fertilization, it ramifies into a group of semi-independent chains or pathways. While these causal streams have some effect on one another, they are fairly independent. Moreover, we often can usefully distinguish the sexual maturity pathway from the somatic maturity pathway. In virtue of the relative independence of these pathways, evolution can involve changes in the timing of one with respect to the others. That is heterochrony. So, for example, paedomorphic evolution is the relative acceleration in descendent taxa of the sexual maturity pathway; peramorphic evolution is a relative acceleration in the descendant of the somatic maturity pathway.

Raff (1996) argues that heterochrony has been considerably oversold as an evolutionary mechanism (for the opposite view, see McNamara 1997). Even so it is widely accepted that one source of evolutionary novelty is relative changes in developmental timing. Human evolution is a notorious example of (alleged) paedomorphosis—the retention of juvenile characteristics into sexual maturity. Allometry is an allied phenomenon that may also be important. As organisms become more massive, there are changes in the ways physical forces impact upon them. Very light animals have trouble not flying. To them falling is no danger. As organisms grow, more of their cells are hidden away on their inside, and their thermal profile changes. The strength of bones and other structural supports is roughly a function of the area of their cross section, yet load tends to be a function of the organism's volume. For these reasons and many more, larger organisms are not just scaled-up versions of smaller ones. So for clear functional reasons, body proportions change in growth, though these allometric relations go beyond these functional requirements. In consequence, phenotypes can be altered, sometimes quite dramatically, either by shutting down growth early or by prolonging it. McNamara develops a nice example of this phenomenon in his discussion of horn shape and size in the bushbuck/nyala/kudu group of African bovids. As we move to the larger species, horns do not just grow relatively larger but they are also more elaborately spiralled in a quite regular pattern (McNamara 1997, 146–150). Heterochrony here interacts with allometry to create the possibility of variation.

The existence of developmental constraints, and their importance in biasing the evolutionary trajectory of a lineage, is relatively uncontroversial, though the same is not true of the identification of particular constraints and evaluating whether they are hard or soft. Since novelty is just constraint's inverse, equally, the importance of developmental biology to the explanation of novelty is uncontroversial. So an interactionist conception of evolutionary change which gives weight both to factors internal to

a lineage and to the role of the environment is close to a consensus view in evolutionary biology. In the rest of this paper I will discuss some ideas about development that are both much more speculative in themselves, and which if accepted would cause more of a shift in the evolutionary consensus.

3. Beyond Consensus Interactionism. “Adaptationism” is a label for a number of quite different doctrines.⁹ One of these is the idea that adaptation presents evolutionary biology with its critical phenomenon; the phenomenon that most needs explaining. Selection is the key feature of evolutionary change because only cumulative selection explains adaptation. As Godfrey-Smith puts it, selection answers evolutionary biology’s \$64K question: why are organisms adapted? One message we can take from recent work in developmental biology is an alternative view of evolutionary biology’s “hard problem.” On this alternative view, the critical problem facing evolutionary biology is to explain the *evolution of evolvability*. Evolvability, in turn, rests on two pillars. The first is the evolution of a developmental toolbox that is partly shared across the phyla. The second is developmental modularity.

There is a suggestion from some in developmental biology that evolutionary history has been characterized by the invention of a few critical developmental subroutines which are then reused repeatedly in the development of many very different adaptive complexes. Thus Gilbert et al. suggest that

The information content or determinacy of a complex anatomical structure is orders of magnitude higher than that of the genome, and such order rises from the use of standard parts, which are arranged hierarchically and which can interact with each other. (Gilbert et al. 1996, 367).

Along similar lines, Muller and Wagner, in reviewing the different morphological uses of Hox genes, note that

The more we learn about molecular mechanisms of development in widely different organisms, the higher the number of conserved mechanisms that become known. Some of them do indicate homology of morphologically divergent characters . . . Still others illustrate that highly conserved molecular mechanisms may be used in radically different development contexts, indicating that the machinery of development consists of modular units that become recombined during evolution. (Muller and Wagner 1996, 11)

9. For a good taxonomy, see Godfrey-Smith forthcoming.

An obvious but very important example is the invention of cell types. For the most part, animals do not differ from one another because they are built from different sorts of cells. Rather, they build different structures from similar cell toolkits. This seems to be a quite general phenomenon: developmental processes and the genes and gene complexes that regulate them often seem to be deeply conserved and widely shared in metazoan evolution. The homeobox story is a paradigm case of the conservation of developmental tools, but it is only one such case. The mechanisms for initiating eye and limb formation (Gilbert et al. 1996, 366) seem to be others. Notice though that it is tools not outcomes that are conserved. In arthropods, homeobox genes determine segment identity; in vertebrates, they play a role in the development of neural crest cells (Raff 1996, 190). Since in both cases they are implicated in segment differentiation along the back/front axis, they play the same kind of role. But the structures they build are very different.

The suggestion being floated here is that phenotypes are being generated by a complex interaction between relatively few developmental mechanisms. Explaining these mechanisms and how they can be combined is central to understanding evolution. The suggestion here is not, of course, to deny that adaptation is a real and important phenomenon. It is, rather, to argue that the complex adaptations we find in the metazoa rely on the evolution of the developmental tools that make complex adaptation possible—on the evolution of evolvability. On this view, explaining evolvability rather than the existence of adaptive complexes becomes evolution's "hard problem." Once we have explained the tracks in morphospace that the evolvability of a lineage makes accessible, explaining adaptation would be relatively straightforward. The limit position here might be that of Goodwin: developmental constraints make so few tracks in morphospace available that selection has little to do (Goodwin 1994).

There is a second element in this view of the evolution of evolvability, namely, developmental modularity. Consider the fate of the idea of developmental entrenchment. Gould (and others) have made much of the alleged conservatism of evolution; he is deeply impressed by the preservation of the distinctive organization of the phyla, and the failure to invent new basic organizations over half a billion years or so (Gould 1991, McShea 1993). Developmental biology provides one standard explanation of this conservatism through Wimsatt's idea of generative entrenchment (Wimsatt and Schank 1988). Developmental processes—especially those of early ontogeny—become entrenched through being causally upstream to very many features of an organism. Thus a change in those early processes is likely to ramify, having many effects on the developed phenotype, and some of these are nearly certain to be deleterious. Extending this idea a little, the more complex the organism, the more it has been elaborated

over evolutionary time, the greater the *phenotypic burden* on these fundamental processes of early and middle ontogeny. So the more evolutionary change there has been in a lineage, the less significant change there can be in that lineage. Only novelties that are alterations to, or graftings onto, late ontogeny are still possible.

Thus the conservativeness of the early, entrenched stages of ontogeny has become almost proverbial. Early development is legendarily stable. For who has not seen Haeckel's famous diagram of the developing embryos of a fish, calf, chick, and human laid out side by side, a diagram showing their extraordinary early similarity (admittedly, touched up a bit!). Of course the development of the early embryo is entrenched, for almost everything is causally downstream from it. So its patterns will be very hard to change. Events in early development have so many causal ramifications that any change is nearly certain to cause something to go wrong.

Plausible though this idea of developmental entrenchment sounds, we know that at least in this simple form it cannot be true. Raff has pointed out that in a number of important groups, the adult body plan has been retained despite major reorganizations of development. In both echinoderms (Palumbi 1997) and amphibians there are many striking examples of "direct development"—skipping the normal larval forms in which the larvae lives and feeds independently. Furthermore Raff shows that we have all been conned by the iconographic Haeckelian diagram (Raff 1996, 195). The "early ontogenetic similarity" of the vertebrates is not early similarity at all, but rather a similarity that arises roughly at a developmental midpoint from very different routes. The salamander, chick, and human go through a stage of similarity on the developmental road from different early development to different late development. Moreover, even if evolution has been conservative with respect to the preservation of the body plan, it has not with respect to the invention of adaptation. Many adaptations requite significant shifts and reorganizations of development. New adaptations in a lineage do not standardly arise by terminal addition. Turtles and tortoises have had their body dramatically reorganized through their evolution of armored protection; whales too are spectacularly changed from their ancestors.

So something must be wrong with the simple form of the idea of developmental entrenchment.¹⁰ This leaves us with a pressing problem.¹¹

10. For Wimsatt's response to this problems in the application of the idea of developmental entrenchment, see Schank and Wimsatt forthcoming.

11. Perhaps it leaves us with two pressing problems. It may be that the "Persistence of Type" is an artifact of our taxonomy rather than an objective feature of the history of life (Ridley 1990, 1993). But if the persistence of old body plans, and the lack of new ones, are real features of life's history, this does call for explanation. One explanation

What is wrong with the reasoning behind the ideas of generative entrenchment and the conservatism of early ontogeny, reasoning that lead us to expect strongly entrenched, hence evolutionarily viscous, developmental programs? How have lineages retained their capacity to sprout new adaptive complexes involving significant morphological reorganization? This has involved not just the invention of developmental routines—how to grow limbs and eyes, how to code front-to-back positional information—but also the modularization of development. An attempt to work out the nature and significance of this modularity is found in the work of Gunter Wagner. This work connects back to the interactionist conception of evolution, for if Wagner's ideas turn out to be right, evolution does not just have preferred tracks (for a given lineage), it has a natural grain as well.

4. Modularity, Homology, and the Grain of Change. Until the recent explosion of molecular phylogeny, the phylogeny of clades was reconstructed largely on the basis of the patterns of similarity and dissimilarity of morphological traits. There is a good, though far from perfect, match between morphological and molecular trees, a match which indicates that this process was not arbitrary. Yet one significant problem within evolutionary theory concerns the individuation of traits. In constructing the family tree of the cats, we count lions, tigers, leopards, servals, but not the cheetahs, as sharing a certain structure, retractable claws. We do so despite differences in the paws of these cats which have the consequence that the exact muscular details will vary from lion to leopard to serval. This is one of the many traits, one of the many homologies,¹² which unify this group. Notice though that this systematic judgment is sensitive to how we taxonomize traits. A more fine-grained taxonomy would treat claw

has appealed to developmental entrenchment. If, however, body plans are stable despite radical reorganization of development, and if conserved genetic and developmental tools can be used to make different body plans, then developmental explanations of body plan persistence seem to be in deep trouble. What then does explain it?

12. The literature in developmental biology tends to use homology in two quite different ways. One is the cladistic concept: the leopard's retractable claws are homologous with those of the tiger, for claw retraction has been invented only once in the feline lineage (I am supposing) and both cats have inherited that adaptation from the ancestor. These two traits are the same because they can be traced back to one and the same (numerically identical) ancestor. But developmental biologists often use the term "serial homology" for structurally repeated elements in the same organism. In this usage, each of my neck vertebrae are homologous with one another. There is very likely some evolutionary connection between repeated elements of this kind. Perhaps the vertebrate making routine was only ever invented once, and each vertebrae is the result of a reuse of this single trick. If so, all my seven neck vertebrates have some kind of genealogical connection. Nonetheless, it is clearly very different from that between tiger and leopard claw control, and it invites confusion to use the same term for each.

control as a series of automorphies, telling us nothing about relations within the cat group or about the relations of the cats to other carnivores. The same would be true of more exotic ways of counting; if, for example, we regarded claw control and paw color as a single trait. A more coarse-grained analysis would miss the distinctive features of cheetahs' paws.

Thus the use of traits in phylogenetic and evolutionary theorizing demands an appropriate individuation of traits and of their character states. But what is the principled basis of that individuation? For many evolutionary theorists, that question has lacked urgency. For there has been within the evolutionary community intersubjective agreement in counting traits and trait changes. However, that agreement is by no means complete. The problem of identifying traits is particularly pressing for those interested in the evolution of behavior. Is human aggression a single trait with a distinctive adaptive explanation? Perhaps this is too coarse and there are instead many different forms of human aggression. Perhaps it is too fine: aggression is just one aspect of a more complex behavioral disposition which sometimes produces cooperation or retreat rather than aggression. The segmentation of an animal's behavior into its components is both very difficult and a prerequisite to any good theory of behavioral evolution. And here there is no tacit consensus as a basis upon which to work.

The "grain problem" is pressing not just in behavioral evolution but in macroevolution as well. In the last decade, S. J. Gould has ignited a controversy by arguing that overall variation in animal body forms has declined since the Cambrian exposition. Animal life occupied more morphospace then than it does now. This soundness of this idea depends on disparity being an objective property and on the way we measure it. Gould has supposed that it is measured by the features we use to distinguish the metazoan phyla from one another, and which divide those phyla into their major subgroupings. This supposition has provoked vigorous debate (Gould 1991, McShea 1993). The disparity problem is at least a close cousin to the problem of objectively identifying traits. For the problem of disparity includes the problem of identifying the dimensions of morphospace. One natural way to picture morphospace is to suppose that the traits of a lineage identify the dimensions of morphospace, and different character states of those traits identify different locations on those dimensions. On that view, trait identification had better be objective, and we ought be able to show the principles behind it. We cannot rely on the intersubjective agreement of taxonomists even where we find it, for such agreement might simply reflect our natural perceptual and cognitive categories.

In a series of papers Gunter Wagner has attacked this problem from a developmental perspective, in defending a "building block" hypothesis.

His starting point is the problem of evolvability: if the development of an organism were thoroughly holistic, with every aspect of a phenotype developmentally linked to many other aspects, then an organism's phenotype really would be developmentally entrenched; it would not be "evolvable." Moreover, Wagner points out that the literature of evolutionary computation shows that the process of generating small random variations in a fairly successful system, followed by selective retention of improvement, by no means guarantees adaptive evolutionary change. You cannot improve your Word 5.1 program by randomly varying its code and hoping to keep and breed from any improvement. One aspect of evolvability is the nature of the adaptive landscape, for the existence of many local optima tends to damp down evolutionary change. But evolvability largely depends on development. Hence the relations between genotype and phenotype which permit evolutionary change have been the subject of a good deal of recent attention, perhaps most famously from Stuart Kauffman (1993, 1995). The basic theme of this work is that adaptive evolution is possible only if small changes in genotype typically cause small changes in phenotype, and these in turn typically cause small changes in fitness. Word 5.1 fails this test: small changes in the underlying program typically have large effects on its performance. In Wagner's view, these developmental conditions on evolvability reduce to the idea that animal developmental systems must be *modular*. The development of traits (or perhaps trait complexes) must be relatively independent of one another. Only then will improvement in one trait not undercut performance in other respects.

Hence Wagner suggests that traits are real, objective, building blocks out of which organisms are built. They typically exist within a species or lineage in a number of variants; these variants, like the alleles of a gene, potentially can replace one another. Wagner conceives of these traits: (i) as typically being under the distinctive influence of a small chunk of an organism's genome (though within that chunk, epigenetic and polygenetic effects are rife); (ii) as being built by integrated genetically initiated developmental cascades. The development of a structure often depends on epigenetic interactions. Thus Wagner argues that the fibular crest in birds (and archosaurs)—an element the strengthens bird legs and compensates for the reduction of the fibula relative to the tibia—is an adaptation that depends for its development on interactions between the bones, cartilage, and tissues involved (Mueller and Wagner 1996, 9). But these complexes are independent of other trait complexes. They are "developmentally individualised parts of the genotype" (Wagner 1995, 286); and (iii) as serving specific, identifiable functions for the organism (see, e.g., Wagner and Altenberg 1996, 971, Figure 1).

The idea that traits have unique and identifiable functional roles, and hence have identifiable effects on fitness strikes me as the most concep-

tually problematic aspect of Wagner's hypothesis.¹³ I think we use traits to identify functions—the questions the environment puts to the organism—rather than vice versa. Thus we will regard mate choice as a single problem for an animal if it is equipped with a specialization for that task. It is not the existence a single problem confronting the organism that explains the adaptive complex, but the existence of that complex that explains why we think of this as a single problem. The environment does not pose a clear and countable set of problems independent of the organism's response to those problems (Lewontin 1982, 1985; Godfrey-Smith 1996; Sterelny and Griffiths 1999, Ch. 11).

Setting the problem of function aside, there is certainly evidence of developmental modularity. Over the last decade or so, it has become clear that there exists ancient, conserved and widely shared genetic and developmental pathways. The Hox genes may be shared in some version by all metazoa. In all these taxa, these genes seem to play some role in front-to-back differentiation and segment identity. Even more amazing is the role of the Pax-6 gene and its homologies. These genes are conserved across different phyla, and despite the great structural differences between vertebrate and insect eyes, the same genes are involved in the development of both.¹⁴ These developmental resources are not just highly conserved and widely spread through the metazoa. The developmental processes in which they are implicated are quite modular. The Hox genes are named for the homeotic mutations in fruitflies that lead to the discovery of this gene complex. These mutations produce complete and well-formed structures in the wrong places. Thus the so-called *bithorax* mutations produce a four-winged fly in which the third segment of the thorax is a replicate of the second segment, the segment carrying the two wings of the wild-type fly. The still more bizarre *Antennapedia* mutations produce flies in which legs appear in the place of antennae. Wagner discusses a still more striking example:

In a remarkable and widely reported study, Halder . . . succeeded in getting extra eyes to sprout on the wings, legs and antennae of *Drosophila* by targeted misexpression of *Drosophila* "eyeless" gene cDNA. The out of place eyes contain the entire eye structures, including cornea, bristles, pigment and photo receptors, and are electrically responsive to light, prompting Halder . . . to suggest that eyeless is a 'master control' for the complex formation of the insect eye. (Wagner and Altenberg 1996, 967)

13. It is also, however, the aspect he discusses least, so I may be interpreting him as making a stronger claim than he intends.

14. Vertebrate and insect eyes are not homologous, but they do develop from homologous regions in their respective embryos (Mueller and Wagner 1996, 7–8).

These are all striking examples of developmental modularity. For aberrant genetic signals initiate a cascade that is completed despite the abnormal location of these processes in the insect's body. It seems reasonable to infer that the normal development of legs, wings, and eyes is developmentally disconnected from the surrounding tissues, too.

However, in general, modularity is not something that developmental systems have for free. There are some traits which depend on simple and direct paths between genes and the phenotype, but in particular with complex traits, modularity, to the extent that it exists, is an *evolutionary achievement*. In principle, developmental modules can evolve in two ways. Independent causal pathways can become integrated by the evolution of interactions between the genes involved and other elements of the developmental cascade. It is not hard to understand why—if the fundamental machinery of development allows it—integration might evolve, buffering development against the effects of genetic and developmental noise, the effects of recombination, and the like. But Wagner is surely right in thinking that the most difficult problem in understanding the evolution of developmental modularity is explaining how developmental independence could evolve. What evolutionary mechanism could select for the severance of formerly integrated aspects of development, allowing aspects of the phenotype to become disassociable one from another?

One option, explored by Richard Dawkins is to opt for high-level selection. Dawkins is not directly concerned with modularity. He considers two aspects of “evolvable” developmental organizations. One is segmentation and other repeated elements. The other concerns developmental symmetries, so that if a gene has an effect on one place on the organism's body, the same effect will be mirrored across an axis of symmetry (Dawkins 1996, Ch. 7), but the idea could apply to modularity as well. Indeed, both segmentation and symmetry may tacitly depend on modularity in development. The suggestion is that lineages with developmental systems that potentially enable them to generate a wider spread of variation are more likely to persist and to radiate than lineages with more constrained developmental systems. This will be true independently of whatever local accident resulted in those evolvable developmental systems in the first place. But this is not Wagner's line. His best bet is to propose that independence evolves under a combination of stabilizing selection on most of the phenotype but directional selection on one aspect of it. Suppose, for example, that a finch lineage is under sustained directional selection on beak shape, but under stabilizing selection on the rest of its phenotype. Heritable variations which tend to sever the developmental connections between beak shape and other aspects of phenotype will be favored. Notice here that nothing in this suggestion depends on the causes of hereditary variation—genetic or epigenetic—or on whether these hereditary causes

are best thought of as a developmental program. It does not stand or fall on any of the distinctive theses of Developmental Systems Theory.

Clearly the Wagner hypothesis is far, far out on limbs both empirical and conceptual. For instance, Gilbert, Opitz, and Raff have recently defended the reintroduction into developmental biology of the morphogenetic field. Morphogenetic fields are regions—indeed, apparently quite large regions—of the developing embryo, which Gilbert, Opitz, and Raff think of as modular. But they seem to be considerably larger chunks than a single organ or organ complex. The same is true of the idea that one developmental package of tools underlies a wide range of different phenotype structures. These ideas do not suggest that developmental units match up with the homologies and adaptive complexes identified by evolutionary biology, but instead suggest a one/many relationship between a developmental map of an organism and a phylogenetic map of it. These ideas are probably rivals to Wagner's building block hypothesis rather than variants of it, despite some similarities between them. But if Wagner's ship comes in, developmental and evolutionary biology would be offering complementary conceptions of an organism. Developmental biology would be offering evolutionary biology something that it really could use. On offer is a principled basis for segmenting the phenotype of an organism in order to (i) identify the components of fitness that contribute to that organism's overall level of adaptation; (ii) identify the appropriate description for the identification of homologies; (iii) identify the variability most likely to be available to a lineage over its evolution; and (iv) identify the dimensions of morphospace with respect to which questions of disparity ought to be evaluated. I cannot escape the thought that this would be too good to be true.

However, if we back off from the specifics of Wagner's hypothesis, there is an important similarity between his work and that of other hybrids between developmental and evolutionary biology. There is a perspective shift in their perception of the central problem of their field; one from specific adaptation to developmental systems which make adaptation possible. This shift involves a common perception that the evolution of developmental modularity is crucial to understanding evolvable developmental systems.

5. An Interim Conclusion. In this paper I have distinguished three lines on the relation between evolutionary and developmental biology.

(1) It might turn out that development does not have much significance for evolutionary questions. If it turns out that the variation/selection/variation/selection cycle can generate phenotypic change in any direction, the mechanisms that underpin phenotypic variation do not significantly bias a lineage's access to morphospace. If that turns out to be the case, though

developmental biology does help explain variability, and though variability is a necessary condition of any evolutionary change, nonetheless development can be treated as a background condition to evolution.

(2) Despite the existence of the variation/selection/variation/selection cycle, it is quite likely that the mechanisms that underpin phenotypic variation do bias a lineage's access to morphospace. If this turns out most often to be the case, the evolutionary trajectory of a lineage is explained by both factors external to a lineage and factors internal to it. Internal factors include the population structure of species, their interaction with and accommodation to their physical environment, and factors that bias the generation of variation. In virtue of the importance of biased variation, there are deep connections between evolutionary and developmental biology.

(3) Perhaps a proper appreciation of developmental biology does not just contribute to the answers evolutionary biologists seek. It changes their questions. On this view, the most fundamental question that confronts evolutionary biology is, how is the evolution of complex adaptation possible? As we have seen, there is a way of responding to this problem which suggests that the agenda of received evolutionary biology is complementary to a developmentalist perspective. If Wagner's "building block" hypothesis turned out to be right, many organisms are mosaics of units in which function, developmental integration, and genetic support are bundled together. If this were so, the segmentation of an organism that flows from considerations of development and evolvability and those motivated by adaptationist and phylogenetic concerns would pretty well match. Adaptationist and phylogenetic analyses would be given developmental underpinnings. But a developmental segmentation and an evolutionary segmentation may not line up so neatly. We have seen a suggestion from Raff and others that adaptation is dependent on the prior invention of developmental tools that are reused repeatedly, and that underpin many different phenotypes. On this view, adaptation is a real phenomenon, and is rightly explained by selection, but it is made possible only by very special developmental scaffolding. The bedrock agenda of evolutionary biology is to provide an explanation of the evolution of that scaffolding.

These alternatives differ in their empirical bets about development. The jury is still out on those empirical issues. We cannot assume that the existence of widely conserved developmental and genetic resources amounts to the discovery of biases on evolvable variation. For conserved developmental function does not imply the developmental freezing—or anything like freezing—of body plans. One of the most striking features of the discovery of these widely shared developmental and genetic mechanisms is the variety of developmental outcomes they give rise to, often via gene duplication followed by modification. I do not think the agenda of

Developmental Systems Theory, with its emphases on the multifactorial nature of development and the importance of nongenetic inheritance, and its skepticism about the idea of a development program, is central to assessing these bets. So I do not see any fundamental conceptual problem for evolutionary biology on any of these three views.

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