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TWO CONCEPTS OF CONSTRAINT: ADAPTATIONISM AND THE CHALLENGE FROM DEVELOPMENTAL BIOLOGY*

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The so-called “adaptationism” of mainstream evolutionary biology has been criticized from a variety of sources. One, which has received relatively little philosophical attention, is developmental biology. Developmental constraints are said to be neglected by adaptationists. This paper explores the divergent methodological and explanatory interests that separate mainstream evolutionary biology from its embryological and developmental critics. It will focus on the concept of *constraint* itself; even this central concept is understood differently by the two sides of the dispute.

1. Introduction. Controversy has surrounded the so-called “adaptationism” of mainstream neo-Darwinian evolutionary theory during the past two decades. It has been argued that mainstream adaptationists systematically exaggerate the prevalence of adaptations in biology and are insensitive to possible nonadaptational explanations of biological phenomena. One alleged flaw in adaptationism is the failure to adequately recognize *developmental constraints*. This paper addresses the nature of the debate between adaptationists and advocates of constraint.

Most philosophers have learned of the adaptationism disputes from Gould and Lewontin (1979). While this article has attracted much discussion, for various reasons it does not focus philosophical attention on the issue of developmental constraints. It proposes a variety of grounds for distrusting adaptationism, including general methodological flaws. Developmental constraints are among the topics, but are not dealt with in particular depth. Philosophers are familiar with the methodological topics (e.g., falsifiability) and many are familiar with the topics from mainstream population genetics (e.g., genetic drift and pleiotropy) cited by Gould and Lewontin. Their article has been interpreted to claim that adaptationism is unfalsifiable. Various responses both by pro- and anti-

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adaptationists point out that unfalsifiability is an inappropriate criticism of a research program, and that individual adaptationist hypotheses are indeed frequently falsified. (Actually Gould and Lewontin have accused neither adaptationism-qua-research program nor individual adaptationist hypotheses of unfalsifiability. They rather claim that when such hypotheses are falsified, other adaptationist hypotheses take their place. What seems never to be falsified is the belief that the trait is an adaptation of some kind.)

The philosophical discussions of falsification and drift were of unquestionable value, but left the core of the developmental constraint/adaptation conflict virtually unnoticed. Many people question why this conflict exists since, on many descriptions, the processes of natural selection and the processes of embryological development are perfectly compatible, indeed complementary.

From one perspective, the three alternatives of developmental constraint, adaptation, and drift form an ordered sequence. Developmental constraint tends to restrain selective adaptation, and adaptation tends to restrain drift. To believe that (almost) all biological traits are adaptations is to believe that natural selection is powerful enough both to *overcome* constraint, and to *resist* random drift. In this sense, natural selection is a conservative force, a constraint, with respect to drift. Antonovics and van Tienderen (1991) are perplexed by talk of “selective constraints” on drift, but the concept is natural given the dynamics of the situation. We must only keep in mind that selection is not a *developmental* constraint.

From another perspective, these three alternatives are not so smoothly ordered. Mathematical population genetics is at the core of the Modern Synthesis. Genetic drift is perfectly possible, given the formulas of population genetics. Experiments and field studies are required to determine the relative importance in the natural world of selected and drifted traits. So the Modern Synthesis has not been uniformly adaptationist from its birth. Drift is a theoretical option, and its advocates have worked within the Synthesis (Gould 1983, Beatty 1986, Burian 1986). Embryology and developmental biology are a different story. Embryology has never been an integrated part of the Modern Synthesis. This explains its unfamiliarity to most philosophers of evolutionary biology, and why an advocate of developmental constraint would see philosophers’ emphasis on the population genetic alternatives to adaptationism as a symptom of the problem. The neatly ordered series “developmental constraint, adaptation, drift” includes two phenomena (adaptation and drift) that share a common scientific vocabulary, history, and mathematical formalism. The third phenomenon belongs to a field of study that has been isolated from the others during the entire history of the Synthesis. V. Hamburger (1980), an embryologist whose career began in the 1930s, described the Synthesis as

having treated the processes of ontological development as a “black box”, the contents of which can be safely ignored. B. Wallace (1986), a major Synthesis biologist and student of Dobzhansky, recently asked, “Can embryologists contribute to an understanding of evolutionary mechanisms?” (p. 149). His answer was, not much.

In one of the few philosophical papers dealing with the tension between neo-Darwinism and embryology, K. Smith (1992) has discussed two degrees of developmental criticisms of neo-Darwinism. The radical “process structuralists” believe that little of the Modern Synthesis is worth saving. The moderate “general structuralists” believe that a new Developmental Synthesis is needed to integrate embryology and development on the one hand with the neo-Darwinian Modern Synthesis on the other. To its advocates, this new synthesis would be as far-reaching as the synthesis of Mendelian genetics and Darwinian natural history which originally formed the Modern Synthesis (Horder 1989; Gilbert 1991, chap. 23). The present paper will not be fine-grained enough to discriminate among developmental critics according to how harshly they view the Modern Synthesis, but will concentrate on the contrasts between “general structuralist” approaches and the Synthesis.

Developmental constraints are one of the principle topics on which developmental biologists have criticized the adaptationism of neo-Darwinism. An influential and accessible introduction to developmental constraints is Maynard Smith et al. (1985). R. Burian’s contributions to that article are an exception to philosophers’ lack of interest in development. The paper is a multiple authored cooperative catalog of various kinds of constraint (not all of them developmental) along with guidelines on how to classify them. It states the now-standard definition, “A developmental constraint is a bias on the production of variant phenotypes or a limitation on phenotypic variability caused by the structure, character, composition, or dynamics of the developmental system” (ibid., 266). A problem with this paper, for philosophical purposes at least, is that it is too cooperative. The reader gets no feeling for the contentiousness of the issue. Why should the significance of these constraints be questioned by neo-Darwinian adaptationists? To understand, one must look to other sources which more openly express criticisms of neo-Darwinism from the developmental biologist’s viewpoint. (Representative works are Goodwin et al. 1983, Bonner 1982, Thomson 1988 and Gould 1980. For more radical critiques, see Løvtrup 1987 and Goodwin 1984.)

The constraint/adaptation dispute is unlikely to find a quick resolution due to a deep contrast in explanatory strategies between the adversaries. As a step toward explicating the complexity of issues which play a role, this paper will explore two distinct versions of the central concept in the dispute—the concept of *constraint*. The close attention I give to divergent

“meanings” of the term comes not from a hope of reducing the debate to a semantic one—this is not at all a semantic pseudoproblem. A better model for the present study can be seen in E. Mayr’s (1980, 20ff.; 1982, 742ff.) discussion of the various meanings attached to the term “mutation” in the years preceding the Modern Synthesis. Mayr shows that the Mendelian geneticists and their Darwinian naturalist adversaries used the term with distinct meanings which now illustrate the deep theoretical differences. Understanding one’s adversary’s theoretical approach was impossible with this mismatch. Achieving a synthesis required overcoming this difference (as well as many others). As in the mutation case, the divergent meanings of “constraint” fit neatly into divergent theoretical interests and commitments. The dispute is, at bottom, a clash of explanatory strategies, of approaches to explaining the nature of organic life. Charting the two meanings of constraint is not merely a semantic exercise, but an attempt to explicate the structure of the constraint/adaptation dispute. If a Developmental Synthesis actually occurs, future historians may comment on the divergent concepts of constraint just as Mayr has discussed the pre-Synthesis differences on the term “mutation”.

2. Constraints as Acting on Adaptation. The term “constraint” implies some sort of restriction on variety or on change. In the adaptationism debates, what is being constrained? This question has two answers. The most common is that adaptation is being constrained. Developmental constraints, on this view, are restrictions placed by the mechanisms of embryology (for example) on the adaptive optimality of the adult organism. Natural selection simply cannot overcome the conservative forces of development, and suboptimally adapted traits and organisms are the result. The view of constraints as restrictions on adaptation is expressed in Stephens and Krebs’s (1986) discussion of optimality models in foraging theory. Optimality models have three elements:

1. *Decision Assumptions.* Which of the forager’s problems (or choices) are to be analyzed?
2. *Currency Assumptions.* How are various choices to be evaluated?
3. *Constraint Assumptions.* What limits the animal’s feasible choices, and what limits the pay-off (currency) that may be obtained. (Ibid., 5)

The “currency” chosen for a model is some property presumed to contribute to fitness but which can be directly measured. In foraging models the currency might be “Maximization of long-term average rate of energy intake”. The model builder constructs a set of external and internal constraints, and then makes an a priori calculation of the foraging behavior which would optimize the currency given the constraints. External con-

straints are features of the environment which might limit the currency, such as the availability and distribution of the food resource. Internal constraints are features of the organism itself, such as the nature of its perceptual system. If the organism is discovered not to behave according to the optimal foraging model, there is a search for other unnoticed constraints which could account for the suboptimality of the actual behavior. It might be discovered, for example, that a bird which chooses a poor food source when a rich one is available is simply unable visually to discriminate the two food sources. When this new (internal) constraint is introduced, the behavior may become optimal—that is, optimal *within the constraints* (ibid., 180).

From this line of thought many adaptationists conclude that the advocates of constraint have no argument. Other practitioners of neo-Darwinian adaptationism are less explicit than optimality theorists in how they specify constraints, but none of them believes that organisms can just evolve whatever they happen to need, at the drop of a hat. Thus, it is said, constraints are already openly recognized by adaptationists.

Using this conception, developmental constraints are simply one sort of internal constraint. Developmental constraints are *constraints on adaptation*. On this reading, the grounds for conflict between developmentalists and adaptationists is clear. Advocates of developmental constraints believe that adaptationists overlook some factors which limit adaptive optimality. Testing for optimality is more difficult when one is dealing with morphological traits than with behavior patterns, of course. But in principle the resolution of the case is the same. First, prove that a morphological trait is less than optimally adaptive. Then trace the suboptimality's source. If the source is unchangeable in the developmental system, we have discovered a developmental constraint. Moreover, we have shown that the trait is adaptively optimal (within that constraint). Far from refuting adaptationism, this example shows that adaptationist hypotheses are necessary *even for the discovery* of constraints. Stephens and Krebs reject Gould and Lewontin's criticism of adaptationism on precisely these grounds, "Even if they serve no other purpose, well-formulated [adaptationist] design models are needed to identify constraints: without a design hypothesis there would be no basis for postulating any kind of constraint!" (ibid., 212).

3. Constraints as Acting on Organic Form. As plausible as the above interpretation of constraint may sound, constraint-on-adaptation does not accurately express the challenge to adaptationism which comes from developmental biology. Phylogenetically evolved adaptations qua adaptations are the primary explananda of natural selection, the central mechanism of neo-Darwinian theory. In contrast, developmental biology does

not identify phylogenetic adaptations *or any derivative* of adaptations (e.g., constraints on them) as its primary explananda. Advocates of developmental constraint have a different notion than constraint-on-adaptation in mind. This can be seen in P. Alberch's (1982) proposed thought experiment:

[L]et us assume that the morphology of an organism can be described by two variables, x and y . If one plots all the observed forms, a distribution of the kind shown in Figure [3.1] is observed. That is, the observed forms are a subset of all possible forms. Furthermore, the observed forms are arranged in clusters, each cluster corresponding to a distinct species (e.g., *Drosophila melanogaster*) or to a class of pheno-deviants (e.g., *D. melanogaster* wingless mutant). How do we explain the empty spaces and the ordered pattern in morphology-space? There are basically two extreme explanations: a) empty spaces represent nonadaptive forms that have been eliminated by natural selection; and b) they are a reflection of the developmental constraints operating on the system, i.e., there are morphologies that cannot be produced by the developmental program. (P. 317)

To contrast the two hypotheses, Alberch proposes a hypothetical experiment in which all of the members in one of the clusters in the real world (figure 3.1) are allowed to reproduce for many generations while the forces of selection are reduced to a minimum (random mating imposed, no competitive interactions) and variation is increased as much as possible by mutagens. Lethal teratologies would also be logged to keep track of selection at embryonic stages. According to hypotheses (a) and (b) above, what patterns of descendent morphologies would one expect to find? Figure 3.2 represents the two possible outcomes: **H1** is (a), the hypothesis that selection explains all gaps—without selection, morphologies would no longer be clustered; morphospace would be smoothly filled; and **H2** represents (b), the developmental constraints hypothesis. Most of the clusters of **H2** are similar to those which had existed in figure 3.1, one cluster of which (cluster **A**) had formed the ancestors of the organisms in figure 3.2. The additional smaller clusters are (according to Alberch) those which would be unfit in the real world, and so presumably had been removed by selection from figure 3.1. Most of the empty space in figure 3.1 still remains in **H2**. According to **H2**, relatively little of the empty area outside of the clusters in the morphospace of the real biological world was cleared (or blocked) by natural selection. These hypotheses are acknowledged to be extremes, but Alberch clearly leans toward **H2**, “In the second case the role of selection is basically stabilizing, being responsible for ‘pruning out’ the nonfunctional morphologies, and for determining the differential survival of morphological types (states **A**, **B**, **C**, and **D**

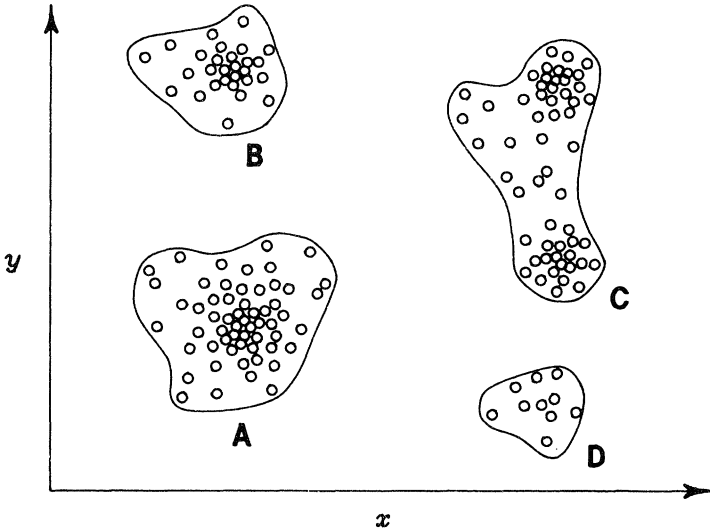


Figure 3.1. The clustering of organisms in morphospace. From P. Alberch's "Developmental Constraints in Evolutionary Processes" in J. T. Bonner, (ed.), *Evolution and Development*. Copyright © 1982 by Springer-Verlag. Reprinted by permission.

in Figure [3.1]). However, the realm of possible morphologies is basically determined by the internal structure of the system" (ibid., 319). Morphospace is generally recognized as clumpy at all levels of the genealogical hierarchy. Birds and mammals cluster separately with open space between the clusters; so do felines and canines, and plants and animals.

This is a dramatic statement of the constraint advocate's position. However, let us note the following about the diagrams. Compare Alberch's drawings with the adaptive landscapes introduced by S. Wright, among the most familiar of evolutionary diagrams. Figure 3.3 is a sample. Two of the dimensions of an adaptive landscape represent abstract genome-space, so to speak, just as Alberch's x and y represent abstract morphospace. The third dimension is represented by the contours, which connect genome-points (or gene combinations) of equal adaptive values. The peaks are areas of high fitness or adaptive value; the valleys, areas of low fitness. One thinks of a population being driven up an adaptive slope as natural selection increases the frequencies of alleles of high fitness.

At first glance, the clusters in figure 3.1 may have been interpreted as the familiar peaks of an adaptive landscape, and the empty areas as the valleys. This is not Alberch's intention. To "see" adaptive peaks in the morphological clusters of figure 3.1 is to *assume H1*, the adaptationist

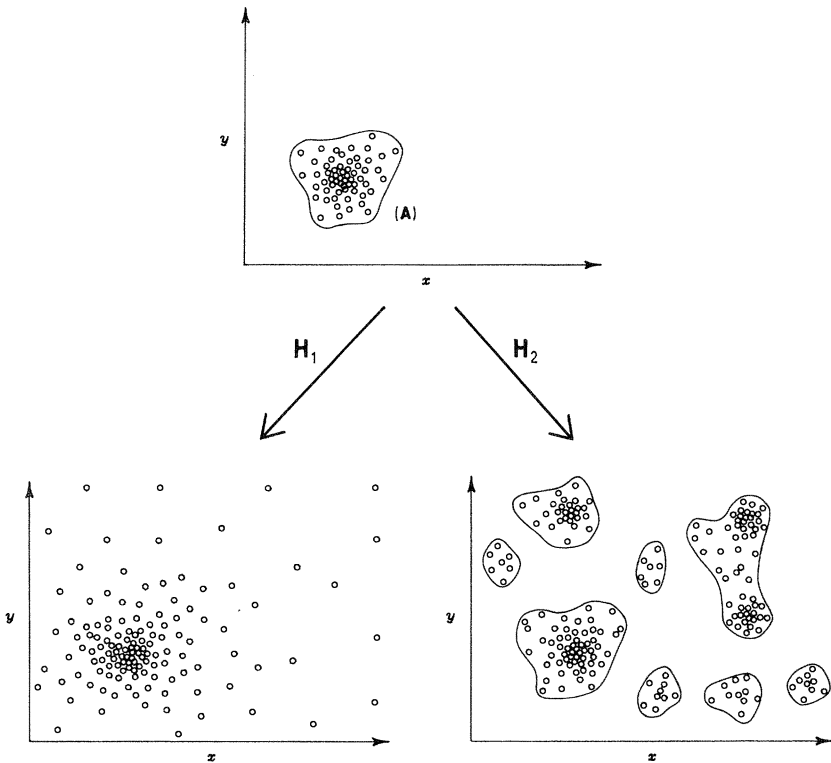


Figure 3.2. Two hypotheses on the effects of removing natural selection from a population. From P. Alberch's "Developmental Constraints in Evolutionary Processes" in J. T. Bonner, (ed.), *Evolution and Development*. Copyright © 1982 by Springer-Verlag. Reprinted by permission.

explanation of the clustering of existing morphotypes. Alberch's drawing includes no dimension to represent the adaptiveness of morphotypes. It is purely a diagram of organic form. Indeed, **H2** specifically denies that adaptivity is responsible for the clumpiness of the morphospace. Another way of understanding this point is to think of the adaptive surfaces in figure 3.2 as absolutely flat, having been flattened by Alberch's removal of selective forces. Hypothesis **H1** exhibits the pattern of variation which an adaptationist would expect to evolve on a flat adaptive landscape.

Unlike the main currents of neo-Darwinism, developmental biology does not focus its explanatory attention on adaptations *or on their absence*. Rather, developmental biology aims to explain *organic form* and its origins in the embryo. The explanandum is not adaptation, but form. Constraints thus proposed by developmental theorists are not constraints on adapta-

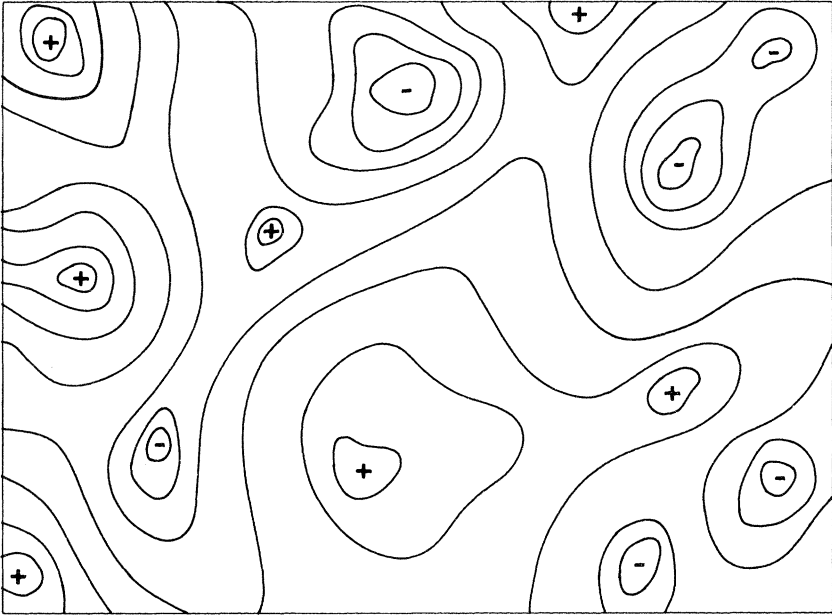


Figure 3.3. An example of an adaptive landscape in the sense of S. Wright. The x and y axes would represent genetic space. Contour lines connect points of equal adaptive value; plusses and minuses are areas of high and low adaptivity.

tion, but *constraints on form*. Many other pictorial representations of the ranges of possible morphology can be found in the literature of developmental biology. The drawings contain no dimension representing the relative adaptivity of the “permitted” and “forbidden” forms. Examples are representations of the morphospace of coiled shells (Maynard Smith et al. 1985, 278; Schindel 1990), J. D. Murray’s (1981) reaction-diffusion model of mammal coat color patterning, and the drawings of permitted versus forbidden digit patterns frequently cited by students of the vertebrate limb (e.g., Alberch 1982, Holder 1983). Not natural selection, but rather the embryological mechanisms of growth are believed to permit or forbid these forms. *Adaptive values are not the evidential basis from which the constraints are inferred.*

To be sure, constraints on form (call them constraints_F) may result in constraints on adaptation (constraints_A). But this is not always or necessarily the case. The relation between constraints_F and constraints_A is not one of entailment, and to mistake the former for the latter is to measure developmental biology using an adaptationist’s yardstick. If the developmentalists’ contribution to the explanation of biological traits is limited

to traits which are known (or asserted) to be non- or maladaptive, then the developmentalist has no business discussing traits believed to be adaptive. But in fact no developmentalist would abandon the field in this way. Developmentalists would claim that their contributions are a proper part of the full explanation of even the most wonderfully adapted trait.

4. Two Approaches to Phyllotaxy. An example illustrates the distinction between constraints_A and constraints_F. Phyllotaxy, a simple developmental system, is the pattern, usually spiralling, of the growth of leaves, bracts, or florets on plants. Examples are helical patterns of leaves on stems, seed covers on pine cones, spiral patterns of seeds on sunflower heads, and florets on cauliflower and broccoli stems. An interesting feature of much phyllotaxy is that various particular patterns can be correlated with the Fibonacci number series. (The Fibonacci series is 1, 1, 2, 3, 5, 8, . . . , 55, 89, 144 . . .—each number the sum of the preceding two.) Particular phyllotactic patterns are associated with fractions in which the numerator and denominator are successive numbers in the Fibonacci series. The denominator indicates the number of leaves between successive exact overlaps as the leaves spiral along the stem. The numerator indicates the number of circuits around the stem before that overlap occurs. For pine cones and sunflowers, it is easier to count the numbers of observable left-hand versus right-hand spirals; the fraction arrived at is equivalent to the circuit-counting method in stems and leaves. The Fibonacci number multiplied by 360 degrees gives the angular deflection from one leaf (bract, and such) to the next in a particular pattern. Plants often start early growth with a low numbered Fibonacci pattern (e.g., 3/5) and transfer to higher numbers (34/55, 55/89) in later and larger stages. The absence of intermediate or divergent patterns, either within or between species, strongly hints at constraint.

Phyllotactic spirals have been discussed at least since Leonardo da Vinci. D. Thompson (1942, chap. 14) sketched that history. One notable attempt to give an adaptationist explanation of Fibonacci phyllotaxy was by C. Wright, the American mathematician and early supporter of Darwin. Wright pointed out that the Fibonacci series converges on an angle called the “golden section”, measuring approximately 137.5 degrees. This angle is an irrational portion of the full circle. If there were successive layerings of radial vectors about an axis distanced by the golden section, no vector will ever exactly overlap a lower vector. So if the phyllotactic angle of divergence were the golden section, no leaf would ever exactly shade any lower leaf from an overhead sun.

Thompson listed five reasons to doubt Wright’s adaptationist explanation (*ibid.*, 932). For example, the higher numbers in the Fibonacci series are close approximations to the golden section, but they are much

rarer among plants than the low-numbered ratios which allow frequent overlaps. Furthermore, the golden section has no special adaptive significance—any angle of divergence which is irrational with respect to the full circle will do the job, and there are infinitely many such angles. So Wright notwithstanding, Fibonacci phyllotaxy seems a good candidate for a developmental constraint.

K. Niklas (1988) studied the influence of Fibonacci phyllotaxy on adaptation. He first cited evidence that the phyllotactic pattern is developmentally conservative, including evidence that within an individual plant or a species it is insensitive to environmental variables, and that it varies among species in a discontinuous manner. He investigated the effects of the various patterns on the amount of sunlight striking the leaves. Using computer simulations, Niklas showed that the photosynthetic potentials of different patterns did indeed vary. This raises the question of why plants would develop according to a less-than-optimal phyllotactic pattern:

Model plants constructed with equal total leaf area and number differ significantly in flux, even when [phyllotactic patterns] are very similar. . . . Nonetheless, computer simulations indicate that a variety of morphological features can be varied, either individually or in concert, to compensate for the negative aspects of leaf crowding resulting from 'inefficient' phyllotactic patterns. Internodal distance and the deflection ('tilt') angle of leaves can be adjusted in simulations with different phyllotactic patterns to achieve equivalent light interception capacities. (Ibid., 12).

Evidence shows that these and at least some other possible nonphyllotactic traits (e.g., leaf opacity, spectral sensitivity) are more amenable to selection than is the phyllotactic pattern itself, and are not developmentally linked to it in such a way as to block their ability to compensate for the "inefficiencies" of a specific pattern.

Niklas concludes that phyllotaxy, while a "candidate" for a developmental constraint, is *not* a "developmental constraint *sensu stricto*". It is rather a "limiting factor". The difference is important, "In the first case, the morphological domain is 'constrained' by the internal structure of the developmental system. In the second case, the system provokes and defines changes in other facets of the organism's development. . . . The distinction between a 'constraint' and a limiting factor is important, because it reflects a measure of plasticity within the developmental repertoire" (ibid., 9). But in the cases being discussed, the morphological domain is indeed constrained as to its possible phyllotactic patterns—only certain patterns are ever available, and they are without variation within a species. The plasticity which exists is not in the "domain" of phyllo-

tactic pattern *at all*—it occurs only in the compensating factors such as stem distance, leaf angle and tilt. When Niklas denied that the “morphological domain is ‘constrained’ by the internal structure of the developmental system”, the domain referred to could not be the positioning of leaves on a stem—that domain *is* so constrained. The intended domain must have included that pattern *together with* the set of traits which compensate for phyllotactically imposed limitations. And why is that group of traits bundled into one domain? Certainly not because they are developmentally integrated—by Niklas’s hypothesis they cannot be. Either the entire morphology of the plant is the morphological domain, or the domain just happens to include ⟨phyllotaxy, stem distance, leaf shape, leaf angle, leaf tilt, surface opacity⟩—that is, the “limiting factor” together with its compensators. Such a domain is defined post hoc by what is needed in order to achieve adaptation. Niklas is measuring development with an adaptationist’s yardstick, and in phyllotaxy he finds no constraint.

Niklas’s notion of constraint is clearly constraint_A, constraint on adaptation. An unchangeable developmental pattern can count as a constraint_A only if it irremediably reduces adaptation. Since “limiting factors” are those which can be compensated for, they are not constraints_A, “[P]hyllotaxy may operate as a limiting factor, provoking compensatory adjustments in other morphological features, but, from the perspective of photobiology, it is not a developmental constraint *on performance*” (ibid., 14; emphasis added). On this concept, two equally canalized traits may differ on whether they count as constraints. A trait which can be compensated for is not a constraint_A no matter how deeply it is entrenched in the developmental program.

Another stance can be taken with respect to phyllotaxy. A developmentalist, with eyes on other phenomena than adaptation, takes an apparent constraint on organic form as *itself* a target for explanation—but of developmental rather than adaptational explanation. G. J. Mitchison (1977) is an example. Mitchison explains the Fibonacci series as a mathematical consequence of certain known or plausible features of stem growth and leaf placement. Positioning of a newly developing leaf is influenced by the positions of the leaves just below it; new leaves cannot originate too close to their predecessors or to the apex of growth. Mitchison develops a close-packing or “touching-circle” model which assumes that leaf positioning is governed by something like an inhibitor mechanism:

This assumes that the leaves and apical tip of a plant produce an inhibitor which prevents new leaves from forming in their proximity. I shall assume that this inhibitor diffuses or is transported away from its sources, and that the new leaf is formed at the first site to appear beneath the growing apex where the inhibitor concentration falls below a fixed threshold. (Ibid., 273)

Mitchison shows that Fibonacci patterns will result from this mechanism, and from many other leaf positioning mechanisms. He explains the Fibonacci number size of the pattern (i.e., 3/5 vs. 89/144) as a function of the rate of growth of the apex of the stem. On this model, the head of a sunflower which shows a dramatic 89/144 Fibonacci number at its perimeter would result from a 30-fold increase in the size of the apex (the growth zone for new bracts) during its growth. The rapid expansion of the sunflower's "apex" can be seen from the fact that the growth zone is the circumference about the center of the flower. Lower Fibonacci numbers correspond to plants whose stems increase in diameter only slightly during growth.

Let us consider Niklas's and Mitchison's results from both the adaptationist's and the developmentalist's points of view. To an adaptationist, Mitchison's conclusions are of little consequence. There is an obvious adaptive reason for leaves not sprouting too closely together, and some mechanism has evolved to keep them apart. Mitchison shows (only) how a broad range of possible leaf spacing mechanisms would produce Fibonacci patterns. But Fibonacci patterns are not the explananda of adaptationist explanation since they are (apparently) not adaptations. The patterns may have turned out to be obstacles to adaptation, constraints_A, but Niklas shows that such obstacles can be overcome. So Niklas's work has the important adaptationist effect of showing that even these nonadaptive, universal patterns need produce no reduction of overall adaptation. What may have been a constraint_A (a constraint *sensu* Stephens and Krebs) turns out to be potentially innocuous (*vis-à-vis* adaptation).

The scene changes from a developmentalist perspective. Niklas produces no explanation of the forms of plants. He takes the existing phyllotactic patterns as a given. In contrast, Mitchison explains how a certain organic pattern comes to exist, given what we know about plant growth. He points out the features of the growth of plants which generate the Fibonacci patterns in all their variety, and explains why non-Fibonacci patterns are rare. The adaptive relation of Fibonacci patterns to the photosynthetic potential of plants is irrelevant to Mitchison's enterprise. The biological functions of leaves or of seeds play no role in the analysis. Whether Fibonacci patterns contribute to adaptation, whether they are "limiting factors" or even absolute barriers to optimality is inconsequential to the correctness of Mitchison's developmentalist explanation. Mitchison intended to explain organic form, not adaptation.

The work of these two biologists is consistent. Mitchison addresses organic form, Niklas, the adaptive effects of that form. In present terminology, Mitchison gives a developmental explanation of a phyllotactic constraint_F, while Niklas shows that the same constraint_F is not (necessarily) a constraint_A. Being primarily interested in adaptation, Niklas ex-

presses his conclusion as the discovery that phyllotactic pattern is not a developmental constraint “sensu stricto”. He is correct in that it is not a constraint “sensu accommodationis” (in the sense of adaptation). But it is still a constraint_F sensu stricto, a genuine constraint on organic form.

The distinction between constraints_A and constraints_F is only implicit in developmental biologists’ discussions of constraint. Nevertheless, Niklas misreads his developmentalist sources. He cites Alberch (1982) in support of his conclusion that phyllotaxy is not a constraint. But neither in the Alberch nor in the Maynard Smith et al. (1985) definition quoted above are developmental constraints defined as *reductions of* adaptation. Adaptation is mentioned in neither of the definitions. It is Niklas’s own adaptationist orientation which fills in the missing reference to adaptation.

So developmental constraints as seen by practitioners of developmental biology are defined by their effects on organic form rather than on adaptation. Such constraints_F surely influence adaptation; the “versus” in “adaptation versus constraint” is not meaningless. But the effects of a constraint on adaptation are secondary consequences of its effects on form, at least from a developmentalist’s perspective. The primary explanandum of developmental biology is the origin of form.

5. How Form Relates to Adaptation. The assumption that constraint on form entails constraint on adaptation seems natural, but I will explore its grounds. Under what conditions do constraints_F create constraints_A? A constraint on potential adaptation will only occur when the variant which is prohibited by a constraint_F *would be* selectively favored *if* that variation were to exist. That is, whether a constraint_F gives rise to a constraint_A depends on whether the environment would selectively favor forms *forbidden* by the constraint_F over forms *permitted* by the constraint_F.

In the real world, which traits fit this description? Which traits are such that their prohibited variants would be selectively favored, were they only allowed to exist? Naturalistic observation obviously will not answer this question—the variation required for observable differential fitness is absent by hypothesis. Some sort of hypothetical reasoning must be invoked. In some cases it would be simple; immunity to a juvenile lethal disease would presumably always be selectively favored over the lack of such immunity. But for interesting morphological cases the assessment might be difficult. Consider the task of comparing the adaptivity of the single proximal bone in the tetrapod limb (humerus, femur) with the adaptivity of a probably-prohibited double proximal bone. The prospects of a well-founded empirical assessment, for the entire tetrapod group or any subgroup, seem dim indeed.

So empirical proofs that specific constraints_F yield specific constraints_A may be elusive. Nonetheless, general theoretical orientations have im-

plications for the issue. What sort of theoretical commitment leads to an expectation that development constrains adaptation? Let us reexamine our trio of theoretical positions in the adaptationism dispute: constraint, adaptation, and drift. Adaptedness is a relation between organic form (or other phenotypic trait) and environment. Adaptedness is a relational, ecological concept. Neo-Darwinism explains states of adaptedness as resulting from natural selection. Natural selection is a two-stage process involving (1) the production of heritable variation; and (2) the winnowing of that variation by environmental demands, with these two stages repeating themselves in each generation. The debates between adaptationists and advocates of drift concern phenomena at the second stage of this process, the ecological level. The core of the dispute is whether each trait is (and has been) under selective pressure during its history. Adaptationists consider the world a demanding place, and believe that even small differences between traits have selective consequences. Advocates of drift consider the world far less demanding. They believe that many variations are effectively neutral in their selective value. (Neutralism and drift are not synonymous, as I will show.) In the absence of selection, the statistical principles of population genetics imply that traits will drift, with the likelihood of a random variant becoming fixed in the population depending on effective population size. The judgements of each side on the adaptive status of current traits (adaptive or selectively neutral) generally matches the historical explanations offered for the existence of the traits (natural selection or products of drift).

Developmental constraints function not at the ecological second stage of the process of natural selection, but the first stage, the production of heritable variation. They bias that production. In the course of studying how organic form is (ontogenetically) produced, developmental biologists believe they have discovered embryological processes which can produce only a certain range of phenotypic variation. The issue is not the amount of variation which is possible, but the range of that variation. A comparison with generative linguistics is helpful here. Just as a hypothesized universal grammar of human languages can generate infinitely many different potential human languages, the generative processes of embryology have an unlimited number of possible variants. But, just as all languages generated by a universal grammar are governed by certain constraints, so are all of the possible outcomes of the embryological processes of a given phylum. The similarity here is not accidental—developmental theories are generative theories.

What would an advocate of constraint_F say about the adaptive status of constrained_F traits? Adaptation is a topic at the second level of natural selection where the winnowing of the less-well-adapted forms occurs. The discovered facts concerning the embryological development of form

imply nothing about the fitness relations between that form and its eventual environment. The existence of strong constraints_F have no immediate implications for the existence of constraints_A. Information about the environment, not just form, is needed before judgements of adaptation are possible. An embryologist qua embryologist has no more to say about the adaptedness of particular organic forms than, say, a climatologist, a scientist on the opposite, environmental side of the relational field of ecology. To be sure, some embryologists (or climatologists) might be interested in how their subject matter ties in with adaptation, but the major research programs of developmental biology and climatology can be conducted in isolation from questions of adaptation. The existence (or not) of constraints_F requires no assessment of the adaptedness of the resulting forms.

Advocates of constraints_F may choose to take a position on the disputes about the second level of natural selection. Justifying any such position would require evidence from ecology, of course (adaptation being an ecological concept). Let us consider the options. An advocate of strong constraints_F may be a neutralist regarding the ubiquity of selective forces. If so, he would expect that many constraints_F would have no effect on adaptedness. After all, the world is a nondemanding and an open place to a neutralist. There would presumably be room for “purposeless” conservatism of pattern just as there is room for “purposeless” variation and drift. For such a *constraint_F neutralist*, constraints_F may well not result in constraints_A.

It was noted above that neutralism was not synonymous with drift. This is why. Some selectively neutral traits might be present in a species because they drifted to fixation, others because they are the products of a developmental constraint. Neutralism is true of both sorts of traits, but drift explains only the first. The almost universal identification of neutralism with drift would seem to be another effect of the isolation of developmental biology from mainstream evolutionary theory.

A different advocate of constraints_F might not be a neutralist at the ecological level of discussion. She might indeed believe that all organic traits have adaptive importance which will be strongly tested by the process of winnowing. But, since this person also believes that strong constraints_F exist, she would believe that almost any constraint_F would likely result in a constraint_A, a reduction of potential adaptation. We might label this person a *constraint_F adaptationist*.

But this sounds paradoxical. Does this argument not pit adaptationists against the advocates of constraint? Well, yes and no. We must tease apart two aspects of the position called “adaptationism”. I propose the following terminology:

Soft adaptationism: All organic traits have adaptive values on which the winnowing process of natural selection operates (or would operate if there were a variant). For this reason a constraint on form is (probably) a constraint on adaptation. Contradicts neutralism.

Neutralism: Many organic traits are adaptively neutral, so a constrained trait might well be adaptively neutral. Contradicts soft adaptationism.

It can be seen that soft adaptationism does not (in itself) deny the current existence of constraints_F; the “constraint_F adaptationist” is a soft adaptationist who believes in constraints_F. An adaptationist who denies the existence of developmental constraints does so by claiming that natural selection can (and has) overcome any such constraints. This position can be called:

Hard adaptationism: All organic traits have adaptive values, and those adaptive values, via the principle of natural selection, provide the proper historical explanation of the existence of those traits. Any developmental constraints can be (and have been) overcome by the forces of natural selection.

The assumption that a constraint_F must result in a constraint_A is soft adaptationism. Hard adaptationism adds to soft adaptationism the claim that selection can conquer any constraint_A. Since selection has conquered any constraints_A and (almost) all constraints_F are constraints_A, selection must have conquered (almost) all constraints_F. (Exceptions would be constrained_F traits which are fortuitously adaptive.) Other soft adaptationists may believe in the continued existence of constraints_F, and believe that the existing constraints_F impose an adaptive disadvantage to the organisms so constrained (as compared with hypothetically similar organisms which lacked the constraint). But such a conclusion does not follow from the existence of constraints_F. It requires soft adaptationism, that is, the denial of neutralism with respect to constrained_F traits.

Let us relate these distinctions to Alberch's and Wright's diagrams. The point of contention between neutralism and soft adaptationism is the shape of the adaptive surface. Soft adaptationists believe that (almost) all points on the surface lie on a relatively steep slope. Neutralists believe that large areas on the surface are flat, reflecting the lack of selection on the range of traits associated with those areas. An advocate of constraints_F (such as Alberch) believes that the distribution of morphologies in the two-dimensional morphospace is to be explained by the processes of embryology and that even on an adaptively flat landscape (like figure 3.2) most of the pattern would remain. So Alberch would not expect the clusters in morphospace to match the contours of the adaptive landscape. But

notice that the clusters may fail to match the adaptive contours in two different ways. First, there may not *be* many contour lines in this landscape, reflecting the neutralist opinion that adaptive landscapes have large, flat plains. Second, there may be many steep contours, but only a weak correlation between the pattern of the clusters and the shape of the adaptive landscape. This second possibility is the “constraint_F adaptationist” belief that constraints_F usually do yield constraints_A; distributions of morphotypes would only partially correlate with contours of high adaptivity. Only the hard adaptationist, who denies both neutralism and the strength of constraints_F, would expect Alberch’s morphological clusters to perch precisely atop adaptive peaks.

This is why the notion that development constrains adaptation arises from adaptationist biology. One must have soft adaptationist leanings even to worry about developmental constraints reducing adaptation.

I do not mean to suggest that soft adaptationism is controversial, or that each of the above positions is equally justified. The Modern Synthesis has successfully and justifiably brought most modern thinkers to the view that adaptation is an extremely prominent feature in the organic world. But it is important to understand the program of developmental biology in its own terms, and not simply in terms of its sometime and oblique opposition to neo-Darwinism. It is mistaken to infer the lack of a constraint_F from a high degree of adaptation in an organism, and it is mistaken to infer a reduction in adaptation from the existence of a constraint_F.

6. Conclusions. The recognition of developmental constraints is only a small part of the revisions to neo-Darwinian evolutionary theory being urged by developmental biologists. Constraints are the point at which the two traditions come closest. As we have seen, even here is a gap; the two sides mean different things by the word “constraint”. Among other topics for which developmental theorists claim superior explanatory resources over neo-Darwinians are long-term evolutionary trends, rapid evolutionary change, parallel and convergent evolution, and the origins of higher taxa. Some constraints_F are even seen as enhancing the possibilities for adaptive changes. It is argued, for example, that the plasticity of certain developmental mechanisms allows for correlated changes in form without the requirement that each correlated part be the target of independent selection (Rachootin and Thomson 1981). Such correlations are still constraints_F since the correlated features must change synchronously. This is incoherent if constraints are defined as restricting adaptation, as they are by adaptationists like Niklas, Stephens and Krebs. Developmentalists sometimes recognize that an overemphasis of the term “constraint” gives a false picture of their intended contributions to evo-

lutionary theory. From a group report on a 1981 conference, “Every time that someone mentioned a ‘constraint,’ someone else reinterpreted it as an ‘evolutionary opportunity’ for a switch to a new mode of life, and a third person would bring up the subject of the complementary ‘flexibility’ ” (Horn et al. 1982, 217). It is beyond the scope of the present paper to describe all of these ideas, let alone to evaluate them in comparison to mainstream neo-Darwinian explanations of the same phenomena.

Hamburger claimed the Modern Synthesis treated ontogenetic development as a black box which could safely be ignored by evolutionary biology. Mayr (1991, 8), on the other hand, attributed the nonparticipation of embryologists in the Synthesis to the embryologists’ own disinterest. Both are probably correct. Blame need not be assessed here, especially since the bracketing of the complexities of development was probably a necessary condition for the remarkable achievements of the Modern Synthesis. Fifty years after the Synthesis, the role of developmental biology may need reappraisal. The developmental biologists’ arguments should be seen as assertions that the bracketing of development should end, that the insides of the black box of development have causal relevance to evolutionary biology.

Even though the constraints issue is not the most exciting aspect of developmentalists’ theoretical ambitions, the semantic confusions exposed above strongly prejudice the argument. For example, recall the statement by Stephens and Krebs that claims of constraint presuppose adaptationist research, that “without a design hypothesis there would be no reason to postulate a constraint!” Taken as a claim about constraints on form, this statement is blatantly false. The patterns in Alberch’s morphospace diagrams are based on a knowledge of form alone, not on a discovery of suboptimal adaptivity. The forbidden morphologies of digit patterns are determined not from surveys of the digit patterns which actually occur in nature, but from a knowledge of the developmental processes which build those digit patterns. Murray’s constraints on color patterns are proposed on generative, developmental bases alone—adaptationist design hypotheses are not consulted. It is false to claim that constraints on form are discovered by embryologists in the same way constraints on optimal foraging are discovered by ethologists. Developmental biology is a source of knowledge independent of adaptationism.

Classifying developmental constraints as constraints_A has a second pernicious effect. It trivializes the detailed causal understanding which developmentalists believe is essential to evolutionary biology. An example can be seen in Dawkins (1982). Here are listed a number of explanations for the imperfection of adaptation. They include time lags (the environment might have changed too recently for natural selection to have operated), the variability of environments (an organism cannot be perfectly

adapted to every microenvironment), costs and materials (birds cannot grow wings of titanium alloys), and “available genetic variation”. Developmental constraints fit in this last category. As Dawkins puts it elsewhere, “no mammal will ever sprout wings like an angel unless mammalian embryological patterns are susceptible to this kind of change” (1986, 311). These are indeed factors accepted by neo-Darwinians which would explain imperfection of adaptation. The operation of these constraints_A in any given case would presumably be determined in the manner of Stephens and Krebs—by discovering imperfect adaptation—rather than by a prior causal understanding of the process which *produced* the constraint. Even though here and elsewhere Dawkins acknowledges the complexity of embryology and the limits it places on the available genetic variation, the actual insides of the embryological black box remain irrelevant to his discussions. Something is in that box, it is complicated, and it reduces available genetic variation. But its exact details do not matter to evolutionary biology. Variation which is lacking because of details of the developmental process is no more important than variation which by chance just has not occurred.

In other words, the consequence of treating developmental constraints as constraints_A is that the black box can remain closed. The box can be alluded to as the source of an identifiable constraint on adaptive perfection, not unlike the changing environment. The detailed causal accounts which fill texts and journals of developmental biology need have no more relevance to evolutionary biology than the theoretical details of what causes earthquakes, hurricanes, or ice ages. In contrast, advocates of a Developmental Synthesis are asking for much more than a mere acknowledgment of adaptive imperfection. They want to integrate the complex and internal details of embryology into the study of evolution. The significance of developmental constraints cannot be reduced to the language of adaptive imperfection.

In this way the debate between the Modern Synthesis and its developmentalist critics is similar to another great black box debate in twentieth-century science between behaviorists and their opponents who favored cognitive and neurological theories. There are many dissimilarities, of course; issues like intentionality and consciousness are (fortunately) not central to evolutionary theory. But just as Synthesis adaptationists deny the causal importance of embryology to evolutionary theory, behaviorists deny the causal importance of internal states of the psychological organism, either cognitive or neurological states (see Amundson and Smith 1984; and Amundson 1989, 1990 on similarities in debates within psychology and biology). Neither adaptationists nor behaviorists actually deny complex goings-on inside the embryo or inside the brain. They claim that the important scientific issues are understandable without the need for a

detailed knowledge of the intervening processes. Neo-Darwinian evolutionary theorists know that genes somehow build phenotypes and then get winnowed and passed on as a result of phenotype/environment interactions. Likewise, behaviorists know that somehow an organism's stimuli (including reinforcing stimuli, and such) connect with responses, and that the connecting involves lots of complicated interactions among neurons. But just as the details of neurological or cognitive processes are seen as irrelevant to the explanation of behavior, the details of development are seen as irrelevant to evolution. All that matters are the input-output characteristics of the black boxes. Genotypes determine phenotypes, and stimuli are connected to responses. That is all that needs to be known about the insides of the processes to behaviorists or neo-Darwinians. Developmental biologists, like cognitivists and neuropsychologists before them, face the challenge of arguing for the causal relevance of the insides of a black box.

The above paragraph is intended as an explication, not a vindication, of developmentalist critiques of neo-Darwinism. I do not share the common philosophical prejudice that behaviorism had obvious methodological flaws (see Smith 1986). Furthermore, the bracketing of problematic domains is scientifically respectable. Evolutionary biology was built on a huge black box—Darwin could never have written the *Origin of Species* if he had not wisely bracketed the mechanism of inheritance. All that was required of inheritance for Darwin was that somehow some of the phenotypic variation seen in natural populations is passed on to descendants—the detailed insides of the black box of inheritance could (and did) remain unknown for decades. The Modern Synthesis depended on the surprising realization that Mendelian genetics *was* the insides of Darwin's black box.

The proponents of the Developmental Synthesis have a difficult task. Pre-Synthesis Darwinians at least realized the need for a theory of inheritance, although they doubted that Mendelism was that theory. Most post-Synthesis neo-Darwinians do not require developmental biological contributions to evolution theory. Developmentalists may or may not be able to demonstrate that a knowledge of the processes of ontogenetic development is essential for the explanation of evolutionary phenomena. If they can demonstrate this, and provide well-founded developmental/evolutionary explanations, the result will be a dramatic synthesis of divergent explanatory and theoretical traditions.

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