ON THE EVOLUTIONARY SIGNIFICANCE OF DEVELOPMENTAL CONSTRAINTS

by

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Abstract

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This dissertation seeks to understand the role of developmental processes in the production and modification of organismic form. Of special concern is the manner in which particular developmental mechanisms, or development in general, are said to inhibit the ability of the phenotype to respond to selective pressures or "bias" evolution along certain paths. While the existence of such "developmental constraints" (DC's) are widely acknowledged, their evolutionary significance is hotly debated. Some claim that such constraints "may hold the most powerful rein of all over possible evolutionary pathways," and, as such, set many of the parameters within which long-term evolutionary change ("macroevolution") takes place. (Gould and Lewontin 1979) Others grant that patterns of evolutionary change and stasis *might* indicate the presence of constraints, but natural selection is only temporarily impeded. As such, DC's are not of major evolutionary significance (Dawkins, Dennett, many in evo-devo). Over the course of six chapters I examine the emergence of the debate in Gould and Lewontin (1979), the entrenchment of the "received view" in Maynard Smith et al. (1985) and recent accounts and case studies. Throughout I am critical of adaptationist and "selectionist" accounts of constraints—including Dennett's (1995) and recent practitioners in evolutionary developmental biology (evo-devo). In turn, I offer a more "developmentalist" account that is pluralist insofar as I note the importance of developmental mechanisms alongside that of selection in its various modes (stabilizing, directional, internal). I call my view a "pluralist and organismic process structuralist" account. As part of my view I construct a taxonomy of the different kinds of constraints and their varying evolutionary effects by building upon and critiquing Gould (2002) and the work of K. Schwenk and G. Wagner.

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We have seen that the members of the same class, independently of their habits of life, resemble each other in *the general plan of their organisation.* This resemblance is often expressed by the term "unity of type"; or by saying that the several parts and organs in the different species of the class are homologous. The whole subject is included under the general name of Morphology. This is the most interesting department of natural history, and may be said to be its very soul.

Charles Darwin (1859, 434)

If externally applied natural selection is the only force required to produce evolutionary change, the developmental processes don't matter except as features upon which selection can act. If internal organization and processes govern modes of change, then development must be incorporated into any complete theory of evolution.

Rudolph Raff (1996, xviii)

The details of the embryonic developmental process, interesting as they may be, are irrelevant to evolutionary considerations. Konrad Lorenz has put this point well.

Richard Dawkins (1976, 62)

[...] to think of science merely as an accumulation of facts is very misleading. In biological science, and this is perhaps more true for evolutionary than for functional biology, most major progress was made by the introduction of new concepts, or the improvement of existing concepts. Our understanding of the world is achieved more effectively by conceptual improvements than by the discovery of new facts, even though the two are not mutually exclusive.

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INTRODUCTION

I. Introduction

> The central problem for evolutionary biologists interested in development has been how morphology is transformed in evolution. In 1922 Walter Garstang made the very basic observation that because morphology of animals arises anew in each generation, evolution of new animal forms has to be viewed as a problem in the evolution of *development* [my emphasis]. (Raff 1996, 23)

The dominant view in contemporary evolutionary biology holds that the history of life is the history of successive generations of populations of organisms as they struggle to respond, or "adapt," to the demands posed to them by the often harsh conditions of existence. This process is called adaptive evolution and the principal cause of this continuous series of eliminations and modifications is called "natural selection."

This dissertation seeks to understand the role of developmental processes in the production and modification of organismic form. Of special concern will be the manner in which particular developmental mechanisms, or development in general, are said to inhibit the ability of the phenotype to respond to its conditions of existence ("selective pressures") or "bias" its evolution along certain paths. (Schwenk 2002) While the existence of developmental constraints (DC's) is widely acknowledged, their evolutionary significance is hotly debated. Some claim that such constraints "may hold the most powerful rein of all over possible evolutionary pathways," and, as such, set many of the parameters within which long-term evolutionary change ("macroevolution") takes place. (Gould and Lewontin 1979, 86) Others grant that patterns of evolutionary change and stasis *might* indicate the presence of constraints, but natural selection is only temporarily impeded. As such, DC's are not of major evolutionary significance. This is the view of many "selectionist" adaptationists. Adaptationism holds that a biological being is a configuration of features or "traits," each of which is shaped so as to enable an organism to better meet the demands posed to it by what Darwin famously called the "conditions of existence." Adaptationism tends to be genocentric, externalist (focused on environmental selective pressures, not internal developmental processes, as the key evolutionary agents) and is dominant on the contemporary scene. In contrast, "developmentalism" holds that the internal (developmental and structural) organization of living beings plays a determining role in the production and evolution of organismic morphology and tends to restrict or frame the manner in which organisms to adapt to their immediate surroundings. Developmentalists tend to be organocentric and "internalist," and it is with this group that I cast my fate.

The mission of this dissertation is 1) to understand the recent and controversial emergence of the debate over developmental constraints and their relationship to other kinds of constraints. Such a categorical effort I refer to as a "taxonomy of constraints" and this leads to a range of related issues including an examination of the conceptions of trait, organism, adaptation, selection, body plan, morphospace and development itself. 2) To chart the consensus view that emerges in the mid-1980s and the evolution of it and the debate until 2001 or so with attendant criticisms concerning both the positions espoused and the direction of the debate itself. 3) To argue that after the emergence of the new subfield evolutionary developmental biology, much of the DC's debate is now able to better situate itself within a much larger discussion over how to understand the relationship between developmental and evolutionary processes, and subsequently, the role of developmental biology in contemporary evolutionary biology. However, as it turns out, the DC's debate has been somewhat displaced. I shall explain why this has happened and why this is bad. I conclude by offering my own "taxonomy of constraints" and argue for the necessity of a more developmental approach in order to continue to explore the many-leveled relationship between developmental processes and natural selection in the production and modification of morphology. My own view falls within the parameters of what is called "process structuralism" or developmental evolutionary biology ("devo-evo"). Following Sterelny and Griffiths, I define process structuralism as the view that 1) the space of all possible phenotypes (morphospace) is highly constrained, and 2) many of the organizational features of organisms are explained by intrinsic physical constraints such as those resulting from developmental processes. (Sterelny and Griffiths 1999, 232-3)

The structure of this dissertation is as follows. There are six chapters. The first two are centered around Gould and Lewontin's widely-cited polemic, "The Spandrels of San Marco and the Panglossian Paradigm: a Critique of the Adaptationist Programme" (1979) and surrounding debates, figures (especially Dennett), issues, and articles. I begin with this essay because not only does it in large part mark the contemporary beginning of this debate, but it raises the issue of developmental constraints (DC's) in the context of a critique of adaptationism's view of the power of selection and the causal and structural relationships among functioning organisms, developmental systems, and the individual traits they possess. (Chapter One). In Chapter Two, I consider the alternative framework that Gould and Lewontin introduce but do not fully develop. I call this framework the "structuralist approach" and their specific model for an organismic and "structuralist" evolutionary biology the "*Bauplan* Paradigm." In Chapters Three and Four I examine the radical narrowing of the scope of the debate and the construction of what has come to be regarded as the consensus definition of DC's as a "bias" in the production of phenotype (Maynard Smith et al. 1985), and the many problems that arise. I identify Alberch as an underaddressed figure who further develops the structuralist approach, a necessary background condition for appreciating the significance of DC's. Also of importance is the subsequent distinction between constraints on form and constraints on adaptation made by Amundson (1994) (CH4). Chapters Five and Six address the most recent theoretical musings and maneuverings after over ten years of research into what is now called "evolutionary developmental biology or "evo-devo." Here I lay out my own process structuralist taxonomy of constraints and connect it back to controversies first laid out in Chapters One and Two over the relationships among developmental processes, trait change, and selection in the organismic context. I also lay out the split between evo-devo and devo-evo and argue that the division in research programs should be preserved, contra many calls for a "synthesis." Gould's (2002) is also addressed.

II.1 The Basic Tenets of Darwinian Evolution and Contemporary Adaptationism

In the history of thought concerning the nature of living beings two themes dominate: adaptation and diversity. First, all living beings possess features that enable them to survive relative to the circumstances in which they find themselves; that is, they are adapted. This point, which is so obvious as to border upon the tautological, has been appreciated since at least Aristotle. (Mayr 1982, 87-91) The second theme concerns the staggering array of organismic features and their functions: feathers and hair for thermoregulation, claws for grasping prey, beaks that break open nuts, fins for swimming and so on. Each illustrates how a property of some organism enables it to not only meet the demands posed by the conditions of existence, but often wonderfully so. Indeed, the intricacy of the interlocks between organisms and their environment led some to proclaim the world a well-orchestrated harmony in which each organism was designed, by God, to play a part. This was the view of "natural theology." The exquisite fit between wasp and orchid was but one example of how the "hand of the creator" designed an organism's morphology so as to perfectly enable it to carry out critical survival or reproductive functions relative to the uniqueness of its niche. (Mayr 1982, 103-6)

Darwin, of course, put forward an alternate explanation of adaptation and diversity and, in the process, changed the conceptual structure and research programs constituting evolutionary biology. It is generally agreed that there are roughly five separable elements composing Darwin's scheme. (Kitcher 1993, 11-57; Mayr 1982, 505-10)

1) Variation/Diversity: at any stage in the history of a species, there will be variation among its members

2) Scarcity: at any stage in the history of any species, more organisms are born than can survive to reproduce

> 3) Differential Fitness: some of the variation noted in 1) will lead to differences in the relative ability of organisms to survive and reproduce (this effect is spurred on by conditions resulting from "2)")
>
> 4) Inheritance: most of an organism's traits are inherited from its ancestors
>
> 5) Natural Selection: the mechanism by which change occurs such that organisms bearing some characteristics are more likely to survive and reproduce than those possessing other characteristics.
>
> (Kitcher 1993, 19)

As Kitcher points out, "virtually all of Darwin's opponents would have accepted 1-4," and some, if not most, even granted the existence of something like natural selection *within* a species (1993, 20; see Mayr 1982, 477-534 for a slightly different picture of Darwin's contemporaries). Thus, "what was in dispute was not so much the truth of 1-5 as their *significance* [my emphasis]." (Kitcher 1993, 20) Clearly, competition and the scarcity of resources combined with the power of natural selection had much more significance for Darwin than his contemporaries. Darwin's opponents denied that selection was capable of modifying organisms such that species membership could be altered. Once one is a member of type "x", one is always a member of type "x". (Mayr 1982, 511-3) Put another way, what was denied was not the existence of selection, but its power. Darwin's understanding of evolution as a continuous set of transformations and/or "splittings" (speciation)—together with the trimming of various buds and branches (extinction, etc.)--results from a nontrivial claim about the power of gradual modification (selection) to bring about *trans*formative changes usually over vast stretches of geological time. Such a genealogical view is in direct opposition to such essentialist typologies which stressed the "fixity of the species." (Kitcher 1993, 20) Thus, a change in the purported significance of a particular process led to a change in the understanding of the history of life on this planet. Indeed, the implications of this "change in significance" are among the most notorious in the history of Western intellectual life and that requires no more comment here. In any case, the Darwinian core spelled out above remains in place today though it has been modified and greatly expanded upon. Its present morph, "adapationism," constitutes the dominant view within contemporary evolutionary biology.

II.2 On Darwinian "Variational" Explanation

As Sober argues, following Lewontin, in his *The Nature of Selection* (1984), Darwin not only introduced a new explanation for the diversity of organic life and its adaptedness to its surroundings, he constructed a new *kind* of explanation. Sober calls this form of "selectional" explanation "variational." (Sober 1984, 147) Indeed, Darwin "redescribed the world so that the very propositions that called for explanation were different from the ones that earlier theories had focused upon." (147) This brought about a change in the logic of explanation, not just the concepts involved. Sober gives the following case to illustrate his point.

Before us we have the following proposition: all the children in this room read at the third grade level. What Darwin asked what not "how did this property come to be in each individual." Rather, he asks of the population of beings: "why is it that this population has this trait rather than some other?"

Sober calls the first form of explanation "developmental." And it was forwarded by one of the most crucial figures of influence of Darwin's day, Lamarck. The debate between Lamarckians and Darwinians is relevant to debates over adaptationism and developmental constraints today, but before entering into that fray, it is necessary to understand the differences between the two forms of explanation.

> Part of Darwin's revolution was to embed the problem of explaining organic "diversity" in a new contrastive context. (Sober 1984, 150)

A developmental form of explanation focuses on how it is that each of the individuals in question has come to possess the properties under investigation. Thus, as Sober puts it, "You may explain why all the children in the room read at the third grade level by showing why Sam, Aaron, Marisa, and Alexander each do." (1984, 149) One could do this by telling the particularities of the history of each: Marisa's parents gave her writing assignments at an early age, etc. But classical developmental theories tend to be less focused on experience, or "environment," as such and more on the "internal" causal mechanisms particular to some individual. As Sober puts it, developmentalists assume that

> the sequence of states an organism occupies is not the fortuitous result of the experiences that happen to impinge. Regardless of wide possible variation in the character and order of experience, the organism will change in a certain way. The

> idea of a developmental pathway [whether in psychology, linguistics, or evolutionary theory] is precisely the idea of regularly occurring changes that are insulated from environmental influence. (Sober 1984, 153)

The relevance of the environmental conditions is dependent upon the causal mechanisms operative within that individual. Thus, as Sober puts it, "the organism's internal state approximates a sufficient parameter in the theory of transformation. [... Thus, these] [p]owerful endogenous constraints make change look more like an *unfolding* than like a buffeting [my emphasis]." (Sober 1984, 153)

The form of explanation employed by Darwinian selectionists stands in stark contrast to developmental form of explanation detailed above. Darwinian selection is a variational form of explanation, and the explananda is a *population* of individuals. Returning to Sober's case, the reason Marisa and the rest read at the third grade level is because possessing that trait is required for entry into the room. (This explanation assumes that individuals don't lose that capacity as they enter the room. (Sober 1984, 149, see also 150)) Changes in the population arise not because individuals *develop* but because they vary. (149) Sober argues that selection does not explain how it is that *any* individual child can read at the third grade level. In that sense, such selectionist explanations are "antireductionist" since "Change in a set of objects is not accounted for in terms of changes in those objects." (155)

For Darwin and the variational form of explanation, "population change isn't a consequence of individual change but of individual stasis plus individual selection." (Sober 1984, 150) The question is no longer: how did this child come to be able to read at the 3rd grade level? It is: why do the children in this classroom read at the 3rd grade level rather than the 2nd grade level? Or, why does this population of mammals have long necks rather than short ones? What has changed is what Sober calls the "constrastive context." (150) Along these lines, "entry into the room" serves as a nice metaphor from the adaptationist perspective since it is sometimes said that organisms must possess certain traits in order to gain access to some environment (niche). Being, or more accurately becoming,[1] adapted means gaining entry or securing one's spot, and this can happen via migration, mutation, and/or reproduction.

Put in a more familiar way, natural selection explains the *frequency* of traits found in a population. This is illustrated in the conjunction of selectional explanations and the adaptationist paradigm: "When adaptationists say that the fittest trait will evolve, they mean the fittest of the traits *actually present in the population*, not the fittest of all the traits we can imagine." (Sober 1993, 120) For Sober, *natural selection does not determine what traits are possible.* In an important sense, neither does selection determine what traits are present in a population. Selectional explanation, in at least some cases, may explain why a trait does not exist: possessors of it failed to gain entry into the room, the trait made the organism unfit. Selection also explains why an individual enjoys a particular degree of reproductive success. (1984, 152) But, says Sober, the properties of morphology, physiology, and behavior all "fall outside of natural selection's proprietary domain. Yet, at the population level, these limitations disappear." (1984, 152) This form of "selectional" or "variational" explanation especially gained

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[1] No individual starts off adapted since obviously each generation must gain entry even if the conditions are the same as the last generation. Mechanisms of inheritance work to insure continued entry.

dominance once Darwinism was reconciled with Mendelian genetics in the middle of last century in what is referred to as the "Modern Synthesis." This variational form of explanation stays with us to today in the guise of "population genetics" and certain varieties of adaptationism. I will argue that it is insufficient for explaining the production and modification of organismic morphology.

II.3 Adaptationism and its Problems: an Introduction

Over the last half century, "adaptationism" has come to dominate evolutionary biology and is widely regarded as the triumphant "received view." This view holds that a biological being is a configuration of features or "traits," each of which is shaped so as to enable an organism to better meet the demands posed to it by the "conditions of existence." A trait's contribution to the fitness of the organism relative to environmental demands is called its "adaptive value." According to this received view, the process responsible for the adaptive value of each feature is natural selection and "the history of life is the history, essentially, of changes in populations of organisms as a consequence of natural selection." (Sterelny and Griffiths 1999, 38) Such gradual, small, and continuous change is also called "microevolution" (more below) and involves changes in appearance in populations or species over generations. Macroevolution or phyletic evolution considers the origins and extinctions of species and grades. (Thain and Hickman 1994, 218) I will be most concerned with phyla and subphyla and less so with species because significant morphological origination and variation happens closer to the more large-scale end of the taxonomic continuum.

When the gene—or gene sequence, complex, or cluster--is considered to be the sole element that selection works upon (the "unit of selection"[2]) such adaptationism is often labeled "genocentric" and often goes by the popular moniker of "neo-Darwinism." Many adaptationists are neo-Darwinians—Dawkins and Dennett are two of the more famous expositors—but others are pluralists or agnostic (such as Vermeij 1987) in regard to the unit of selection. Pluralists argue that selection takes place on two or more of the following levels: the gene, organism, group, clade, or species. However, genocentrism is not just defined by its stance on the unit of selection debate. Oftentimes, it holds that gene sequences or clusters (such as homeobox and Hox genes) are privileged agents in the control of developmental processes. Consequently, such a view claims that it is through the study of the genetic architecture of organisms that ontogeny and phylogeny (macroevolution) can be best understood (Oyama 2000, 50-6)--although macroevolutionary patterns had been ignored by adaptationist views for many decades during and after the formation of the Modern Synthesis in the first half of the 20th century. (Hinchliffe 1994, 163)

Both adaptationism and genocentrism are targets for criticism in this dissertation. In criticizing the latter, I follow in a long line which includes Gould (1977), Gould and Lewontin (1979), Oyama (1985, 2000), Lewontin (1982), Moss (1992, 1998, 2001); Keller (1995), Raff (1996), Neumann-Held (1998, 2001), Newman and Muller (2000), Robert (2001) to name just a few. It should be emphasized, however, that the two are not

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[2] A "unit of selection" is "whatever natural selection ultimately distinguishes between and whose frequencies thereby not only change but may as a result be causally responsible for changing frequencies of characters in the population." (Thain and Hickman 1992, 437) In this dissertation the unit of selection debate is not of central concern though the causal role of genes in character production (i. e. development) is. See especially CH4-6.

necessarily connected. There are well-known non-genocentric adaptationists (Vermeij 1987) and genocentric developmentalists (Raff, Arthur). My view is critical of adaptationism and genocentrism in each of their combinations and permutations, including supposedly developmentalist appropriations and those who implicitly argue that evolutionary developmental biology is principally a matter of and for developmental genetics (Raff 1996, Arthur 1997). In sum, the confrontation with adaptationism has two fronts, the first is between the "old school" adaptationists and rival developmentalists and "structuralists." (Chapters One and Two) The second front concerns divisions arising among those who accept that a developmental perspective is necessary (adaptationists included), but disagree over the causal origin and evolutionary significance of constraints, the power of selection, and, even the conception of "development" itself. The first front is much broader in scope than the second, but the second goes to the heart of the debate over the future of evolutionary biology (Hall 2000) and occupies the bulk of this dissertation. The next sections lay out the details of the mission and conceptual architecture of the dissertation and define several central themes and concepts.

III.1 The Structure of My Position, Key Categories and Concepts: Structuralism, Development, Morphospace, Body Plans, Phylotypic Stages

The subject of this dissertation is twofold: the first is organismic morphology, especially the *patterns* of evolutionary stasis and change exhibited by the 35 or so different body plans and their key features over the last 530 million years in the Animal

Kingdom.[3] The second concerns the developmental *mechanisms* involved in the production of these morphologies.[4] The mission of this dissertation is to understand the relationship between these *patterns* that have persisted over great lengths of evolutionary time (macroevolution) and the role that developmental *processes* play and have played in their production and persistence. Or to put the previous sentence in terminology used above, of particular focus is the ways in which development is said to limit or bias the production of phenotype and, consequently, the efficacy of natural selection. The position I construct to address this debate is both "structuralist" and "developmentalist." I have discussed the latter briefly in the above, so next is an introduction to structuralism followed by a long explication of development.

III.2 Structuralism

Since its origin in the early 19th century, structuralism has sought to uncover the laws and/or processes that govern morphology. By "morphology" I mean the study of animal form.[5] This includes both the shape, size, and structure of parts (cells, organs,

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[3] Though I do discuss some plant cases in Chapter Four, the overriding focus is on the Animal Kingdom, especially the phyla *Arthropoda*, *Chordata*, and *Mollusca*. This is the focus/bias of the literature and much of the experimental work is on these phyla as well. Because of their more complex structures, the subphyla *vertebrata* receives more attention than others.

[4] As such, the focus is not so much on animal behavior (ethology) but primarily upon structures and functions (geometric and functional morphology) especially in regard to those aspects of phenotype which characterize membership in a (sub)phyla (e.g. the tetrapod limb) and the arrangement of such features into body plans (more below).

[5] More specifically, functional morphology studies the ways in which structure causes, permits, or constrains the function or performance of organisms. "Biomechanics uses the principles of engineering and physics to analyze form and function. Eco-morphology studies the correlation of organisms form and function with their environment," and evolutionary morphology "explicitly aims to integrate development, ecology,

fins, limbs) *and* the spatial arrangement of parts, the organism's "geometry" or "architecture" as it has historically been called. (Thompson 1942) Morphological topics of particular interest include: the configuration of features characteristic of each phyla (its "body plan" or "*Bauplan*"); the developmental stage at which the groups of cells responsible for the production of those major features are present and aligned in accordance with their relative position in adult morphology (the "phylotypic stage"); and the conservation of the structure of individual parts as they undergo functional modification (homology), as in the case of the tetrapod limb which has been modified to fulfill quite different functions such flying in bats, galloping in horses, digging in moles, and grasping in humans. Yet, the limb retains the same structural plan in each (more below). Also at issue are the patterns of change and stasis characteristic of each of these morphological levels. For example, arthropod body plans vary in number of segments but not in regard to whether they are segmented or not; all arthropods are segmented. Vertebrate phylotypic stages vary in regard to the relative length of the tail bud but all vertebrates possess tail buds at this midpoint in development despite having different embryonic environments (e.g. cows on land, fish in the sea). As such, "Selection would seem to have little role in maintaining phylotypic stages under such disparate circumstances." (Raff 1996, 196) And, the tetrapod limb varies in regard to digit number but forelimbs are always composed of two bones.

What is of interest, then, is not just the forms that have been produced, but the *range* of this production (variation), and, consequently, the forms *not* produced.

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biomechanics, and phylogenetic analysis to answer questions about the evolution of organismal complexity." (Futuyma 1998, 519) My focus is primarily upon evolutionary morphology and biomechanics, less so on functional, and very little on eco-morphology.

Explanations for such absences are manifold. Some structures never emerged because they would violate physical law; that is, they are prohibited by "physical constraints." For example, contra the Wizard of Oz, vertebrates cannot possess wheeled appendages because blood cannot circulate to a rotating organ. (Gilbert 1999, 898) Others have never emerged despite the fact that they violate no known physical law and they would contribute to an organism's reproductive success (fitness) in some environment past or present. That is, they *would* be highly adaptive. For example, why are there six-appendaged insects but no six-legged vertebrates? (Raff 1996, 321-3) Again, it does not seem that selection would prohibit such a number of appendages since it is easy to construct realistic scenarios in which such a vertebrate would do well in a number of existent niches. Indeed, being able to run like a horse and have a set of hands free to shoot arrows and steal loot ala centaurs seems a sizeable adaptive advantage over "run-of-the-mill" tetrapods. (Raff 1996, 295)

Yet, over the 400 million year history of tetrapods, no such morphology. Why not? At least three explanations are possible. The first is that such a morphology would make no contribution to fitness. It would not pass the selectionist's test. This option is ruled out for the present case. Second, not enough evolutionary time has elapsed and/or the right amount or kind of genetic variation has not emerged. As such, six-legged vertebrates and many other heretofore never produced morphologies could, in principle, emerge. Therefore, it is not a "law of nature" that prohibits such creatures unlike the case of Dorothy's rolling vertebrates, it is a historical accident, a true evolutionary contingency, that the genetic variation required is absent for our quasi-centaurs. The third explanatory option splits with the first two and invokes the developmentalist perspective so crucial for this dissertation. The next section considers this perspective, and after that explication, locates the domain and problems of explaining evolutionary morphology relative to a developmental perspective.

IV.1 Development

> If externally applied natural selection is the only force required to produce evolutionary change, the developmental processes don't matter except as features upon which selection can act. If internal organization and processes govern modes of change, then development must be incorporated into any complete theory of evolution. (Raff 1996, xviii)

The third explanatory option follows a weaker version of the "law of nature" argument discounted in option two above. Put simply, whereas adaptationist approaches focus on the contribution each trait makes to the overall fitness of an organism, developmentalist approaches seek to understand the causal mechanisms responsible for the generation of such traits. This leads to further exploration of the capacities and limits of such mechanisms and the manner in which they may be modified (in the "field" or the lab) so as to change the range of phenotypic variation. As in Sober's distinction between variational and developmental forms of explanation above, while the dominant population genetics approach seeks to explain evolution in terms of changes in gene frequencies in populations over time (Sterelny and Griffiths 1999, 38), developmentalists seek to understand the role various ontogenetic processes at different levels play in the production of phenotype, patterns of gene expression included.

Put most simply development is the production of phenotype—all those features an organism "exhibits," or, whatever is not the genotype. Also called epigenesis or ontogeny, development involves the coordination of all those processes and elements that go into the production and reproduction of an organism. This coordination is sometimes characterized as "hierarchical" (more below). An *evolutionary* study of development looks at the ways in which changes in phenotype can be explained by appealing to changes in ontogenetic processes. As Gould put it, "Evolutionary changes must be expressed in ontogeny, and phyletic information must therefore reside in the development of individuals." (Gould 1977, 2)

The explananda of developmental biology are differentiation, morphogenesis (e.g. the production of organs, bones, etc), growth, reproduction, and, more recently, the evolutionary change of such developmental systems. (Gilbert 1999, 2-3) (The discipline *evolutionary* developmental biology, or "evo-devo," isn't much more than a decade old.) This dissertation focuses principally on the last one, particularly in regard to morphology and function, and not so much on the third (reproduction)--or on behavior for that matter. The rest will frequently come up, but due to the morphological focus, morphogenesis gets most of the attention.

Development in the animal kingdom—the kingdom most frequently addressed in this dissertation--though incredibly diverse, generally is constituted by variations upon four themes: rapid cell division (cleavage); the differentiation of the three germ layers ("gastrulation"); the formation of organs ("organogenesis"); and the "setting aside" of the germ cells. (Because knowledge of development is not widely disseminated in philosophy of biology, much less in philosophy of science, throughout this dissertation I will provide much developmental detail when appropriate.) Each stage is be briefly described below:

1/ Cleavage: after fertilization there is a series of rapid cell divisions (mitosis) then the egg starts to hollow itself out as it becomes a sphere (blastula).

2/ Gastrulation: mitosis slows down, and the different kinds of cells (blastomeres) start to move and sort themselves into three "germ" layers. The outer layer (ectoderm) becomes the epidermis and nervous system, the middle layer (mesoderm) gives rise to several organs (heart, kidneys, gonads), connective tissues. and red blood cells, and the inner layer (endoderm) produces the lining of the digestive tube and associated organs (pancreas, liver, lungs, etc.).

3/ Organogenesis: After the germ layers are formed cells start to interact and form-producing fields emerge. These morphogenetic fields produce organs, blood cells, lymph, cartilage and bones and so on. This stage is characterized by much cell migration. In vertebrates it begins with neurulation: the formation of the neural tube which eventually becomes the brain and spinal cord.

4/ Setting aside of the germ cells: in many species, a specialized portion of the cytoplasm gives rise to the cells that are the precursors of the gametes thereby producing and preserving a well-maintained division between the body's (somatic) cells and those which directly contribute to the formation of the next generation.

(adapted from Gilbert 1999, 3-5)

Again, though 1-3 will be addressed in this dissertation, most attention will fix upon those ontogenetic mechanisms which are directly tied to the production of morphology and major organism-level features. For my purposes, "4/" is important only if it has a significant morphological impact.

IV.2 Development, Physico-chemical Processes, Epigenesis

Although the phenomena of development, along with reproduction, distinguish living beings from the rest of the natural world, there is much continuity between developmental processes and physico-chemical processes.

Throughout this dissertation, I shall use the phrase *physico-chemical process* (e. g. positive and negative feedback loops, excitable media, adhesion, mineralization, calcification) to refer to those processes that are not unique to the biological realm. Processes particular to the living realm—e.g. gene expression, gastrulation, osteogenesis—will be referred to as "biological" processes or when appropriate as "developmental" or "epigenetic" mechanisms. It should also be pointed out that although ontogenetic, developmental, and epigenetic are nearly equivalent in meaning and application, epigenetic is sometimes used to refer to developmental components or processes other than those of the genome or gene expression ("epi-genetic") in order to call attention to or emphasize the importance of such processes. I shall follow this usage. As one might expect, there is often overlap between the epigenetic and the physico-chemical, for example, *cellular* adhesion.

The prime roles played by adhesion and excitable media in animal development and functioning are but two examples of the importance of physico-chemical processes. Excitable media are materials that actively respond to their environment in a mechanical, chemical, or electrical fashion such that an oscillation or periodicity emerges. (Newman and Muller 2000, 307)[6] They are found in the living and non-living realms. Not only are such media and materials common in morphogenesis but such biochemical periodicities supply much of the foundation for intra-organismic compartmentalization and segmental tissue organization. (Newman and Muller 2000, 307) Both of these processes are fundamental during and after the formation of the germ layers, a defining moment in animal development.

Another physico-chemical process of major importance is cell adhesion. Cell adhesion is often due to environmental factors. For example, some modern cell surface proteins that mediate attachment between cells do so only in the presence of calcium ions. (Newman and Muller 2000, 306) The reasons for this are not genetic nor is it due to the action of proteins. Rather, it is the presence of calcium ions that makes the cells' surfaces sticky. (306-7) In addition, two of the five modern types of gastrulation in modern metazoans (epiboly and involution) could have originated as simple consequences of such differential adhesion. (307) And, cell adhesion, like excitable media, also plays a critical role in organogenesis. In sum, insofar as animals are multicellular creatures, the significance of adhesion is obvious, and this is true for their

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[6] For example, when Bromous acid is mixed with bromate and cesium, a propagating wave is produced. (Goodwin 1994, 49-52)

early evolution[7] as well as in animals' more recently evolved developmental processes and morphology.

Although animal ontogeny is notoriously complex, many of the components and processes that comprise it are fairly simple and in play throughout the various phyla of the kingdom. As Newman and Muller put it, much of animal morphology is largely a matter of

> molding clusters of dividing cells into physical shapes. Layers, sheaths, tubes, rods, spheres, etc. are formed by aggregates of cells, mobilizing a wide range of biomechanical forces that result from the different properties of different cell types and their extracellular products. (Newman and Muller 2000, 313)

This focus on physico-chemical processes is in alignment with process structuralism's focus on the biomechanical and biochemical, and its efforts to show the significant role of non-selective processes in evolution. (Sterelny and Griffiths 1999, 233)

IV.3 The Hierarchy of Development and Genocentrism

Causation in biology seems to rarely follow the exclusively inside-out model of weak reductionism. For instance, in ontogenetic development causation is

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[7] Indeed, the earliest animals are likely to have been simple cell aggregates that arose by adhesion of originally free-living cells, or by the failure of the same to separate after mitosis. (Bonner 1998, summarized in Newman and Muller 2000, 306) The physical properties of this condensation of viscoelastic "soft matter"—chemically active condensed materials (314)--"will thus have insured the production of a profusion of multilayered, hollow, segmented forms." (306) Newman and Muller call this a pre-Mendelian world of fully or partially interconvertible prototypes for the genetically routinized body plans to come." (309)

> extremely complex with causal loops and reticulations among different causal pathways resulting in a picture that does not fit the simple pattern of reductionism. (Brandon 1996, 189-90)

An organism is generally regarded as a "hierarchically nested system" (Gilbert 1999, 891, Oyama 1995, 514; Raff 1996, 326-7) It is composed of units that are nested sets, coherent within themselves but part of larger units: cells are parts of tissues which are parts of organs which are parts of systems as so on. But, development is not governed by any one component or process. (Newman and Muller 2000). As Oyama states, "The results of these developmental systems cannot be attributed to the formative power of one class of factors whose action is constrained or modulated by other, secondary factors, as traditional schemes require" (Oyama 1995, 514).

Of course, as this passage insightfully points out, to call some process a constraint is to imply that the real agent is elsewhere. Thus, the notion of developmental constraints seems to connote that the true agent of evolutionary change is elsewhere: natural selection's action upon the randomly mutating genome as the most common story goes. This is an assumption that underlies not only adaptationism, but some of its opponents (e.g. genocentric developmentalists).

Oyama argues that there is no privileged level or actor in development, rather there are many "interactants," whose roles shift during development. (Oyama 1995, 514) For example, in early organogenesis a group of cells may initiate (induce) the formation of the eye and then later become heart tissue. (Raff 1996, 205) Genes too play different roles at different times: sometimes they initiate processes and at other times are employed

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by cellular processes … (Raff 1996, xviii, 430) In general, organismic ontogeny is characterized by the fact that 1) the function and role of many participant-agents in the process change over time; 2) "development involves heterogeneous, complexly interacting, and *mutually constraining* entities and processes in which control is distributed and fluid rather than centralized and fixed." (Oyama 1995, 512) On this Developmental Systems Theory model, genes too are "interactants," they "give continuity among generations but can not be said to be the generators of such generations" (512). For Oyama, the previously discussed excitable media, cells, calcium ions, adhesion mechanisms, sheaths, tubes, and rods are all "interactants." There is no centralized command-control center of ontogeny.

Though by no means a commonly held doctrine, (see Sterelny and Griffiths (1999), and Oyama, Griffiths, and Gray (2001) for a recent evaluation and Kitcher's "Battling the Undead" (2001) for a more critical assessment), those elements of DST sketched above—which did not all originate with DST--are coming to be more and more accepted in the developmentalist literature even though much of the "exciting" research is obsessed with supposedly "master regulatory genes" and/or Hox genes. Overall, key works among recent developmentalists (Arthur 1997, Raff 1996) and in developmental biology in general (Gilbert 1999), for the most part portray development as a process composed of many levels and agents, even when research itself may be unduly focused on one level.

The last point in this section about development is that it is comprised of a wide array of components, processes, and mechanisms that are "nested" and thus, in some sense, *hierarchically* arranged. For Newman and Muller, hierarchical means that "Once these macro-shapes have formed," the layers, sheaths, tubes and rods cited above, "their macro-properties in turn become important parameters for further development, not only creating geometric templates and barriers, but also controlling gene activity. " (Newman and Muller 2000, 310) For example, the synthesis of retinoic acid seems to "instruct" cells to join the emerging limb bud (the proto-limb field) by turning on fate-specifying genes in the cells. This recruitment gets the initial outgrowth on the embryo's flank going (i.e. growing). If the synthesis of the acid is blocked the genes are not turned on and limb bud initiation is prevented. (Gilbert 1999, 703-4) The case of retinoic acid fits well with Newman and Muller because it is a naturally occurring oxidation product of vitamin A and thus has causal agency independent of particular genetic or epigenetic mechanisms. In general, these and other factors or "interactants" "are both constraining and generative and are not explicitly specified by "any inherited code of information." (Newman and Muller 2000, 310) Again we see the anti-genocentrism often contained in epigenetic and process structuralist conceptions of ontogeny.

The relations among all the different levels are still not well understood—even protein folding continues to puzzle though a more process structuralist approach seems much more successful. (Newman and Muller 2000, 313) It is clear, however, that causal agency is possessed by each level though to different degrees at different times. For example, in vertebrate limb morphogenesis, lower level units such as Hox genes seem to play a key role in specifying the emerging limb's anterior-posterior axis while the amount of mesenchymal cells available—a factor partially dependent on the global state of the developing embryo—determines the number of digits that will be formed (Newman and Muller 2000, 310-1) (more details in CH3-6)).

What is also clear, however, is that simply appealing to gene sequences and patterns of gene expression does not explain morphogenesis. (Arthur 1997, 95) Developmentalism is then a stark departure from the Modern Synthesis where "evolution was defined as an epiphenomenon of the genetics of populations" (Gilbert et al. 1996, p. 358) and population genetics which "is insensitive to anything like actual developing organisms in their present and historical complexity, for in a population genetic conception of evolution, reliable development is simply presupposed." (Robert 2002, 2, see also my discussion of Sober above.)

IV.4 A Summing Up of the Section: Developmentalists, Adaptationists.

Developmentalists are those that believe that development is a nested and possibly hierarchical system of processes and morphogenetic systems play a key role in macroevolution. For developmentalists, then, there is far more to development than just turning on and off structural genes. (Weber and Depew 2001, 239; Schaffner 1998, 212-3) "Developmental systems," or "ontogeny," refer to all those parts and processes involved in the production of phenotype. This includes various kinds of genes ("regulatory," "housekeeping"), the genomic system as such, different kinds of cells, cellular movements (e.g. invagination), and form-producing (morphogenetic) processes such as those operative in organogenesis. Developmentalist views argue that the range of morphological variation available (see next section) is in part determined by the capacities and/or demands for internal coordination of past and/or existent developmental systems. Absent morphologies, or "missing phenotypes" (Raff 1996, 298-9), are in some cases due not to the absence of genetic variation but to restrictions faced by developmental systems. Such "restrictions" are called developmental constraints.

However, even with this amount of agreement, tension, conflict and misunderstanding persist among developmentalists over the nature of ontogeny, especially relative to selection. Some regard ontogeny as a significant evolutionary force because of the pervasive manner in which it *restricts* organismic responses to selective pressures. This view tends to treat selection as the active evolutionary force and considers constraints as "passive" or "negative" though important (Resnik 1995; Gould 1989; 2002) This view is widely held in evo-devo, though still not given enough attention as I will argue in Chapters Five and Six.

Others regard ontogeny as an evolutionary actor in its own right and for that reason sometimes characterize constraints as "positive" or "active." (Resnik 1995; Gould 1989, 2002). On this view, constraints are creative evolutionary forces that act as "channels" for future variation compelling change in particular directions. This is the dominant view in developmental evolutionary biology (devo-evo) (Hall 2001) and process structuralism. Such a development-centric perspective may even question the characterization that such processes are best described as constraints in the first place. Indeed, process structuralists such as Goodwin and Webster (1996; Goodwin 1994) and Newman and Muller (2000) outline a general theory of evolution which regards morphogenesis as the creative force and genes as the stabilizers. (CH6)

The various stances on ontogeny relative to selection can be categorized as follows:

Conceptions of Ontogeny Relative to Selection

1/ Ontogeny does present a set of constraints, but they are either very few or "breakable" and (mostly) only of short-term significance. In general, ontogeny is under the (indirect or direct) control of selection. (AP, e.g. Dennett)

2/ Ontogeny is a set of more or less binding constraints, a significant number of which pose significant restrictions to selection (AP evo-devo, e. g. Maynard Smith et al. 1985; devo-evo, e.g. Gould and Lewontin (1979))

3/ Ontogeny largely sets the framework in which selection operates (constraints are "positive" or active). The origin of many decisive ontogenetic processes is causally independent of the action of selection (e. g. physico-chemical processes). (devo-evo, e.g. Newman and Muller 2000)

4/ Ontogeny is the primary creative force in the production and evolution of morphology and genes act mostly as stabilizers of the plastic nature of morphogenesis. (devo-evo, e. g. Newman and Muller (2000), to some extent Gould (2002))

(Again, the terms "process structuralism" and devo-evo are equivalent.) As the classifications as evo-devo and devo-evo indicate, the four are not mutually exclusive. However, divisions may be drawn. The AP is committed to "1/" and only "1/." Once one accepts "2/," one is in the developmentalist camp. While those in devo-evo tend to accept 2-4, those in evo-devo are wary of the challenges posed to selection by "3/" and "4/." My own view is situated with those in devo-evo, though there are differences and confusions within this camp as well as I shall discuss in Chapters Five and Six in regard to Schwenk, Gould, and Newman and Muller.

V.1 Morphospace

The next key concept that requires additional explication in this introduction is "morphospace." As briefly alluded to above, morphospace is a theoretical "device" used to elucidate the developmentalist view. The "device" was pioneered by Raup and Michelson (1965), Raup (1966) and later developed by Alberch (1982a, 1982b); see also Amundson 1994) and is used to significant extent by Maynard Smith et al. (1985, 271), Goodwin (1994), Raff (1996, 30-9, 247-55), Eble (2000), and Stadler et al. (2001).[8]

Morphospace is a kind of map—or, more accurately, an *n*-dimensional hyperspace--with a multidimensional metric upon which all possible animal forms could be located.[9] What counts as "possible" is dependent upon the particular conception of morphospace. (Eble 2000) For developmentalists and structuralists, the criteria used to determine position on the map often includes number of cells and cell types, the form of symmetry (radial, bilateral), and number and types of segments and appendages (abdomen, head, limbs, shell, wings, fins, etc.). In this space of all "possible" animal forms (morphospace), an adult's morphology would be represented as a single point. A developing organism, however, would be represented as a trajectory of a particular length and shape since over the course of its existence, an organism passes through a series

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[8] Dennett uses a related notion of "design space" which includes not only the space of all possible animal forms, but the space of everything produced: from organic forms to human artifacts (Dennett 1995, 135-6)

[9] See also Stadler et al. (2001) for more on homology (249), the accessibility of morphospace and how to construct the map (267-9).

forms. And macroevolutionary or phylogenetic changes among body plans "can be represented as departures from an initial trajectory." (Arthur 1997, 247) Also, developmentalists make use of a distinction between regions of morphospace that are either occupied/occupiable, or inaccessible/accessible. Occupied morphospace "can be empirically defined by the cloud of points representing all extant morphologies at a particular moment in phylogenetic history (e.g. the present) or all morphologies that have existed until now." (Arthur 1997, 247)[10]

V.2 Body plan

One popular criterion for organizing the forms in morphospace is the notion of a "body plan." A body plan refers to the major spatio-temporal features of an organism's overall morphological layout. (Physiology and behavior are not relevant.) As such, it is defined not by the subcellular molecular and genetic levels but by supercellular populations of cells in *four*-dimensions. The features that are used to distinguish among different kinds of body plans are type of skeleton (hydrostatic, internal, external); kind of symmetry (bilateral, radial, asymmetric); number of pairs of appendages (0, 2, 3, 4, many); type of body cavity (acoel, pseudocoel, coelem); cleavage pattern (spiral, radial, syncytial); and the presence of segmentation (unsegmented, segmented). (Arthur 1997, 30) The notion of a body plan often corresponds with the concept of phyla (e.g. *Arthropoda*), but the concept may also be applied to subphyla (e.g. vertebrates, beetles). (Raff 1996. 30-1) (More details in Chapter Two.)

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[10] Arthur, following Gould (1991) adds, this would effectively be "an accumulation of all the instantaneous hypervolumes from a starting point which for our present purposes should be the immediate unicellular ancestor of all animals." (Arthur 1997, 247)

Though once controversial (Gerhart and Kirschner 1997, 300-1), it is now widely accepted that thirty-five or so body plans have persisted since the advent of multicellular life somewhere between 1000 and 600 million years ago (*mya*). (Arthur 1997, 81; Margulis and Schwartz 1982) Though in the beginning of the Cambrian period (roughly 550 *mya*) there were a few more body plans (Raff 1996, 96-7), what fascinates is that no new body plan has emerged in the last 500 *mya*--since that Cambrian "explosion" of morphological innovation. (Raff 1996, 181-2; Arthur 1997, 3, 7, 277-84; Gerhart and Kirschner 1997, 296) Adaptationists have failed to explain the persistence of these body plans, the lack of new ones, and much of the range of variation exhibited within each of the thirty-five. (Sterelny and Griffiths 1999, 288-90; see also Goodwin 1994, Raff 1996, Arthur 1997 and *contra* Dennett 1995) In order to address this failure, developmentalists have turned their attention to the particularities of the internal organization of organisms and the possibility that *developmental* processes might lead to *phylogenetic* patterns.

VI. Developmental Constraints: Looking Towards Chapter One Through Four

A central issue of this dissertation concerns the origin and significance of such developmental constraints (DC's). Indeed, much of the current interest in the relation between development and evolution first came to the fore because of the realization that, in some cases, development mechanisms seem to restrict selection's ability to optimally shape traits. After years in the margins assigned to supposedly misguided anti-Darwinian heresies (Dennett 1995, 313-41, Arthur 1997, 85-93), the debate's significance is now acknowledged by many adaptationists (Maynard Smith et al. 1985; Dennett 1995) and is relatively well-established in the mainstream of evolutionary theory. (Gould 1989, 516;

Gilbert 1999, 895-901). Yet, although the *existence* of DC's is granted by nearly all, the *evolutionary* significance of this kind of constraint remains controversial. Many adaptationists remain skeptical, or uninterested (Gould and Lewontin 1979) as developmentalists push for recognition of and further exploration into the evolutionary impact in regard to morphology. My dissertation begins by establishing the context in which the debate of developmental constraints emerges. This is largely done through an explication of various kinds of adaptationism and criticisms of them. Gould and Lewontin's (1979) is central here. (Chapters One and Two.)

I will then argue--beginning in the second half of Chapter Two--that part of the controversy results from confusion since the debate has been plagued by three problems: one, inconsistency in regard to understandings of the origin of DC's and their relations to other kinds of constraints such as physical, biomechanical, and phyletic. I identify this as the "taxonomy of constraints" problem. Two, the failure to distinguish between what is being constrained--morphology or adaptive value (Amundson 1994)--and a related problem concerning a lack of specificity in regard to conceptualizing the relationship between selection and developmental processes (Maynard Smith et al. 1985). Three, the failure to distinguish the "productive" or "positive" aspects of DC's from the "restrictive" ones. (Gould 1989; Resnik 1995) These problems will be addressed in Chapters Three and Four where I begin to offer my own "taxonomy of constraints" (fully presented in Chapter Six), and examine the difficulty of distinguishing between developmental and selective factors, and stress the "productive" aspects of DC's through a more careful consideration of the concept of constraint.

If there are aspects of developmental systems that (partially) shape the course of evolution—the patterns of occupied morphospace--then development would stand alongside natural selection as a critical agent of evolutionary stasis and change, and research into macroevolutionary morphology would require experimental, paleontological and zoological studies (Raff 1996, xiv-xvii). Yet, in their highly influential (1979) essay, Gould and Lewontin draw an even more provocative conclusion. Developmental constraints, they argue, "may hold the most powerful rein of all over possible evolutionary pathways." (86) This claim immediately raises two questions: what causes developmental constraints to arise in the first place? For example, if (some? most? all?) DC's are due to selection, then the existence of such constraints does not pose much of a deep challenge to adaptationist approaches though it may require changes in adaptationists practices (Gould and Lewontin 1979, Dennett 1995). This is the part of the view of the oft-cited Maynard Smith et al. (1985) The second related question is, how can we be sure that such constraints are of evolutionary significance? If DC's arise independent of selection but are usually *overridden* by selective pressures, then, adaptationist approaches may need to widen their scope and recognize the importance of non-selective, developmental factors in evolution, but selection is still in the driver's seat. This is the view of Maynard Smith et al. (1985) and Dennett (1995).

Although I am critical of many of the conclusions drawn by Maynard Smith et al. (1985) (CH 3), and favor a more Alberch-inspired (process) "structuralist" approach (CH3&4), I agree that *methodologically*, determining whether or not particular patterns of variation or stasis are due to particular developmental constraints which are entirely independent of natural selection *may* be difficult. But the problem, I argue, goes beyond mere methodological difficulty, it also indicates a lack of an understanding of the full role that a developmentalist approach can and should play in evolutionary biology. In sum, the debate over developmental constraints has led to the recognition of weaknesses in adaptationism by adaptationists and developmentalists alike. However, by itself, the notion of DC does not constitute a sufficient ground for some alternative approach. But, there is much more to the developmentalist project than establishing the significance of developmental constraints. And perhaps more importantly, developmentalists should not depend too much on the debate over DC's. As such, this dissertation is concerned with the role of development in evolutionary morphology as well as the significance of developmental constraints. In this I am in agreement with Weber and Depew who state, paraphrasing Gilbert, Optiz, and Raff (1996), "we are living in a time when the central problem in theoretical biology is the integration of developmental biology with genetics and evolutionary theory." (Weber and Depew 2001, 239)

The debate over the role of development has attracted the interest of researchers and theorists as diverse as Gould, Dennett, Gilbert, Goodwin, Griffiths and Gray, Amundson, Sterelny and Griffiths, and Oyama. It has led to the integration of a developmentalist approach by adaptationists (Dennett's "reverse engineering approach" (CH2)) and complexity theorists (Goodwin's (1994) morphogenetic fields approach, (Dyke 1988, Newman and Muller 2001). It has also led to the increasing popularity of a novel "general theoretical perspective," Developmental Systems Theory ("DST," see Oyama, Griffiths, and Gray (2001, 1-11)) and the new subdiscipline, evolutionary developmental biology ("evo-devo"). But unlike DST, evo-devo takes up the task of explaining patterns of phylogenetic change, the origin and modification of body plans, and the persistence of phylotypic stages.[11]

VII. Internal Coadaptation, Internal Selection, and the Integratedness of the Organism

> The concept of an embryo is a staggering one, and forming an embryo is the hardest thing you will ever have to do. To become an embryo, you had to build yourself from a single cell. You had to respire before you had lungs, digest before you had a gut, build bones when you were pulpy, and form orderly arrays of neurons before you knew how to think. One of the critical differences between you and a machine is that the machine is never called on to function until after it is built. Every animal has to function as it builds itself. (Gilbert 1999, 1)

The penultimate topic for this Introduction concerns an issue that emerges with much fanfare in Chapters One and Two during my explication and reformulation of Gould and Lewontin's (1979) "structuralist approach" and *Bauplan* Paradigm. Gould and Lewontin (1979, 86) claim that there are stages in development where the action of selection may undermine or disrupt the conditions for selection's existence and/or efficacy by interfering with the base ontogenetic conditions required by such complex (living) systems. By limiting the modifiability of the component elements of the system, the demands of the developmental system itself restricts the power of selection. Some

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[11] Because DST has for the most part not focused on issues of body plans and the macroevolution of morphology, it is not a main concern of this dissertation despite its obvious, and unique and well-articulated, developmentalism. The exception is Wimsatt whose work is discussed in Chapter Five.

DC's arise from the need to maintain such internal integration. The existence and persistence of homologies, body plans and phylotypic stages are cited as other instances of, as well as evidence for, such integration which is part and parcel of the internal organization of living beings.

As discussed above, selection has modified the tetrapod limb in diverse ways, enabling varying groups of this class to radiate into a variety of niches. But as this limb has diverged into avian wings, mammalian legs, and pinniped fins, there has been continued retention of certain bone/joint arrangements. For example, despite all the adaptive divergence, the articulation between humerus and radius/ulna has remained unchanged. Arthur argues that this persistence results from the demands posed by the *developmental* environment (Arthur 1997, 148) rather than by the "external environment" and those traditional conditions of existence such as predation, competition for food, and climactic stress. (219) This notion of *internal* adaptation leads him to postulate the existence of "internal selection" (taken from the forgotten work of Whyte (1965). (Arthur 1997, 148) Arthur argues that the modification of some internal components occurs in order to increase the stability of various ontogenetic processes relative to the developing organism's internal milieu. For example, there is selection for particular developmental genes because of the way in which they interact with other genes not because of their contribution to a trait's ability to adapt to the conditions of its external environment. (148) The same would be said of the persistence of the bone/joint articulations: that they are maintained because the requirements of the internal developmental milieu. Put another way, developmental elements and processes—from genes to modules--are sometimes maintained or modified ***in order to adapt them to each other***. (CH5&6) This

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view counts as a filling out of Gould and Lewontin's (1979) underdefined concept of developmental integration (CH2).

Interestingly, what is of primary interest for Arthur is not the ways in which development restricts selection (see Gould and Lewontin's quote on DC's above), but the ways in which selection operates. Here, a number of questions arise: are certain developmental processes--including the genetic architecture itself--levels or units at which selection can act? Or, is internal selection a different kind of selection—since it has nothing to do with adaptations as a relation between genotype-phenotype and environment? One might quickly respond that a more stable internal organization would seem to increase reproductive fitness in those organisms/populations that bear such traits. But, again, Arthur's developmentalist approach differs from traditional adaptationism because it looks to explain a given trait's contribution to the internal organization of the organism rather than the trait's contribution to meeting demands posed by the environment. Thus, digits are for grasping or digging but the configuration of the humerus and the radius/ulna is for developmental and structural stability.

VIII. A Chapter by Chapter Outline

Chapter One: On Adaptation and Adaptationisms: the power of selection and the nature of the organism

This chapter aims to explain how the notion of "developmental constraint" comes to constitute a critique of adaptationism--the dominant view in evolutionary biology since the Modern Synthesis—especially in regard to the supposed power of natural selection.

(Sterelny and Griffiths 1999, 43-8; Hamburger 1980) In order to achieve this end, I show how current adaptationist approaches—there are at least three—extend and reformulate the Darwinian project. What all these adaptationist views share is the claim that most if not all aspects of organismic morphology are the result of the action of natural selection. Following Gould and Lewontin's seminal essay "The Spandrels of San Marco and the Panglossian Paradigm: a Critique of the Adaptationist Programme" (1979), I argue that the debate over the power of selection also challenges adaptationist understandings of the discreteness of "traits" and the integratedness of the "organism." I have chosen Gould and Lewontin's essay not just because of its wide and positive influence (Sterelny and Griffiths 1999, 43, Sterelny 1995, 196-; Schwenk 1995, 251, Depew and Weber 1995, 477), but because of its provocative contention that the AP's problems are such that an alternative approach is required to either compliment or replace it. The chapter concludes by pointing towards the alternative approach and paradigm that Gould and Lewontin offer (the main object of Chapter Two).

Chapter Two: Structuralisms, Constraints and Development: Gould and Lewontin's *Bauplan* Paradigm and Dennett's Challenge

This chapter continues the criticisms of the AP raised in Chapter One and explores the logic and significance of what I call Gould and Lewontin's "structuralist approach" and their alternative to the adaptationist program, the "*Bauplan* Paradigm" (BP). This is done by focusing upon the different forms of explanation employed by each approach and their respective conceptions of selection, constraint, organism and trait. Gould and Lewontin argue that the organism is a developmentally and architecturally integrated system. This view constitutes both a critique of the AP and an alternative, though incomplete, approach and model.

In this chapter I argue that there is much insight and innovation in Gould and Lewontin's understanding and categorization of those factors that limit the action of natural selection, what I will call a "taxonomy of constraints." Also of significance is the way in which Gould and Lewontin's essay contains many of the seeds of the view that has developed into what is now called "process structuralism." Following Sterelny and Griffiths (1999), I define process structuralism as the view that 1) the space of all possible phenotypes (design space) is highly constrained, and 2) many of the organizational features of organisms are explained by intrinsic physical constraints such as those resulting from developmental processes. The *Bauplan* Paradigm is one version of this view.[12] Yet, inconsistencies and inadequacies in Gould and Lewontin's understanding of the relationship between developmental processes and adult morphology undermine the viability of their scheme and its purported significance.

Ironically, the inconsistencies and inadequacies are most evident in regard to the famous example of the essay, the spandrels of St. Mark's basilica in Venice. However, despite such problems, Gould and Lewontin's approach and paradigm have opened up an important conceptual and methodological space for, at the very least, pointing out critical inadequacies of the adaptationist program in regard to explaining the "deep integration" of developmental processes and macroevolutionary patterns of morphological change and stasis. I conclude by arguing that their most enduring contribution has been to call for non-adaptationist explanations of persistent morphological patterns at the level of

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[12] Goodwin (1994) and Webster and Goodwin (1996), for example, put forward a related but nonequivalent formulation of process structuralism.

development (the phylotypic stage), adult structure (the *Bauplan*), and macroevolution (morphological patterns of stasis and change among metazoans since the Cambrian "explosion" of about 530 million years ago). However, the first two of these gets dropped by the mainstream DC's debate and do not resurface until my Chapter Five.

Chapter Three: Developing a "Taxonomy of Constraints": the Received View and its Problems and a Structuralist Alternative

Though the Gould and Lewontin essay is undoubtedly influential and still oft-cited as both a critique of and/or an alternative to the AP, it in no way constitutes the current received view on developmental constraints. That honor belongs to the nine-authored "Developmental Constraints and Evolution" (1985) which I will refer to by its lead pen, Maynard Smith et al.[13] One reason that the "Spandrels..." essay is not the definitive article is that it is more focused upon *architectural* constraints. However, as I argued in the previous chapter, Gould and Lewontin's taxonomy of constraints is unsatisfactory and crucially confused on the relationship between development and structure. Maynard Smith et al. (1985) aim to solve this confusion, and on this point, I will argue, they are largely successful.

Maynard Smith et al. (1985) have three aims: First, like Gould and Lewontin, the authors attempt a taxonomy of constraints, but whereas the latter focused on the relations among existent components of adult morphology and distinguished between architectural

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[13] Figures as diverse as Dennett (1995), Kauffman (1993), Oyama (1999), Goodwin (1994), Raff (1996), and Dawkins cite Maynard Smith et al 1985 as the definitive article on developmental constraints. The full list of authors is John Maynard Smith, Richard Burian, Stuart Kauffman, Pere Alberch, J. Campbell, Brian Goodwin, R. Lande, D. Raup, and Lewis Wolpert.

and developmental constraints, Maynard Smith et al. (1985) focus upon development and distinguish four different kinds of developmental constraints. Second, like Gould and Lewontin, they address methodological issues and offer three procedures for identifying different kinds of DC's and (third), four additional means for distinguishing the forces of development from the activity of *selection*. They then argue that in the majority of cases, developmental constraints are actually due to the activity of selection alone, or to an inextricable mix of developmental and selective factors.

I will argue that Maynard Smith et al.'s taxonomy is an improvement over the figures addressed thus far because it more fully integrates developmental biology. However, though there is greater clarity and explanatory success in their sketch of the different kinds of DC's, the question of the evolutionary significance of these various kinds is not sufficiently addressed, as they admit. This, I argue, is unsatisfactory. Because of the insufficiency of their account, I draw upon additional works by co-author Alberch who, I argue, offers an alternate view for solving the ambiguities somewhat conceded to by Maynard Smith et al. What is at stake in this debate is not only the explanation of morphological production, modification, and innovation relative to the role of selection, but, as in Gould and Lewontin (1979), our understanding of evolutionary stasis and change, as well as the conception of the organism itself. At the end of this chapter I lay out the first half of my process structuralism. I offer my own taxonomy of constraints in Chapter Six.

Chapter Four: Distinguishing Between Constraints on Form and Constraints on Adaptation

As was argued in Chapter Three, the approach of Maynard Smith et al. (1985) is unable to adequately address the issue of the evolutionary significance of developmental constraints in the evolution of form. Apart from the array of problems discussed in the last chapter, there is an additional reason for the failure. According to Amundson (1994), commentators have failed to note that two different strategies of explanation are employed during these debates. Adaptationists interested in developmental constraints seek to understand the ways in which developmental processes restrict the *adaptedness* of organisms. Developmental biologists interested in constraints seek to understand how they restrict the production of *morphology*. For Amundson, there are, then, two different research programs in operation, and the forms of explanation employed are distinct and in at least one sense, incompatible. Amundson finds this explanatory impasse untenable and concludes by calling for a "developmental synthesis" which would reconstruct the conceptual structure and research program of evolutionary biology by integrating the structuralist approach characteristic among some developmentalists. Amundson's account of the explanatory impasse is largely convincing, especially, as I will argue, given connections to earlier work by Sober (1984). However, his call for a developmental synthesis is so underdeveloped that the viability and desirability of the call is put into question. This issue is fully taken up in Chapter Five in regard to the emergence of what has come to be called "evolutionary developmental biology" (evo-devo). Chapter Four is divided into three parts: The Impasse Between Developmental and Adaptationist Explanations of Constraint, Amundson's Response to the Impasse, and Problems with Amundson's call for a "Developmental Synthesis."

Chapter Five: Part One of the Conclusion: Evo-devo vs. Devo-evo; Functionalism, Developmental Integration and the Limits of Selectionism

This chapter has two aims: first, to explore the claims that evolutionary developmental biology constitutes a response to Amundson's impasse by forging a "synthesis" between developmentalism and adaptationism. The second aim is to show that as the debate has evolved, the category of "developmental constraints" has continued to shrink although controversies concerning their significance continue. I will argue that in regard to claim one, there is no synthesis, but many cross-fertilizations that have resulted in two competing views: an adaptationist "appropriation" and a process structuralist "divergence." As for claim two, I shall argue that there are some positive aspects to the narrowing of the notion (such as the operationalization of the term), but the negative aspects outweigh the positive. In addition, operationalizing the term can be achieved without most of the "narrowing." The notion of "positive" or "active" constraints also comes to the fore in this chapter as I examine the taxonomies of Resnik and Schwenk. Functional "constraints" and their connection to DC's are also discussed.

Chapter Six: Part Two of the Conclusion: My Taxonomy of Constraints and My Pluralist Organismic Process Structuralist Approach (or "POPS")

This concluding chapter lays out the following: a criticism of selectionist attempts to explain developmental integration, my own taxonomy of constraints and its virtues, the paradox for developmentalists resulting from Gould's notion of "cross-level spandrels," and the final details of my own outline of a process structuralist approach to development and evolutionary morphology. Its sections are the Functionalist Challenge from Evo-devo: ESC's and the limits of Internal and External Selection; My Taxonomy of Constraints; On the Special Status of Active Constraints: Gould's Cross-level spandrels" and Newman and Muller's theory of Epigenesis; My Pluralist Organismic Process Structuralism.

CHAPTER ONE:

ON ADAPTATION AND ADAPTATIONISMS: THE POWER OF SELECTION AND THE NATURE OF THE ORGANISM

This chapter aims to explain how the notion of "developmental constraint" comes to constitute a critique of adaptationism--the dominant view in evolutionary biology since the Modern Synthesis—especially in regard to the supposed power of natural selection. (Sterelny and Griffiths 1999, 43-8; Hamburger 1980) In order to achieve this end, I show how current adaptationist approaches—there are at least three—extend and reformulate the Darwinian project as laid out in the Introduction. What all these adaptationist views share is the claim that most if not all aspects of organismic morphology are the result of the action of natural selection. Following Gould and Lewontin's seminal essay "The Spandrels of San Marco and the Panglossian Paradigm: a Critique of the Adaptationist Programme" (1979), I argue that this debate over the power of selection also challenges adaptationist understandings of the discreteness of "traits" and the integratedness of the "organism." I have chosen Gould and Lewontin's essay not just because of its wide influence (Sterelny and Griffiths 1999, 43), but because of its provocative contention that the Adaptationist Programme's problems are such that an alternative approach is required to either compliment or replace it. The chapter concludes by pointing towards the alternative approach and paradigm that Gould and Lewontin offer (the main object of Chapter Two).

I.1 Introduction

In late 1970s, Stephen J. Gould and Richard Lewontin--both independently well-known for their works in paleontology and genetics/comparative zoology respectively--teamed up to pen an essay not even twenty pages in length which over the ensuing two decades caused quite a stir among many who study evolutionary biology, from the researchers to the philosophers (Sober 1993, 142). The essay is significant for two reasons: 1) its critique of adaptationism as both a theoretical framework and a methodology and practice; 2) the alternate approach that it offers. This chapter will focus on the former, Chapter Two explains, assesses, and modifies the latter.

For Gould and Lewontin, adaptationism is the view that an organism is an assembly of complex parts or "traits," each of which makes a contribution to the reproductive success (fitness) of the organism. Each trait, and the organism as such, is largely the way that it is because of the action of natural selection. For Gould and Lewontin, there are three main problems with the "Adaptationist Program" (AP): 1) its conception of trait is "atomistic" and ignores or misunderstands the integratedness of organismic architecture. 2) It overestimates the power of selection as an optimizing agent; 3) The AP fails to conceptualize and investigate other developmental and structural factors that shape the morphology of organisms.[14]

This chapter proceeds as follows: first, a brief background on the concept of adaptation after the rise of Darwinism. Next is a detailed explication of what Gould and Lewontin call the Adaptationist Program relative to other contemporary views. As far as

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[14] Again, in this chapter and dissertation I shall be concerned only with morphology and functions related therein, not behavior.

possible, I try to eliminate and/or modify inaccurate elements of their characterizations so as to avoid any accusations that an irrelevant or fallacious straw man is attacked. Towards this end, I supplement Gould and Lewontin's portrayal with the writings and views of relevant practitioners within adaptationism. I go on to argue that although Gould and Lewontin do not fully appreciate the range of views *within* the AP, their criticisms apply to all three versions. The chapter concludes by showing how the authors' criticisms carve out a space for an alternative "structuralist" approach which focuses upon developmental processes and the organism as an integrated system (the main project of Chapter Two.)

II. The Basics of Adaptation

Organisms are dizzyingly complex beings composed of components and processes operating with great intricacy at a variety of levels, from polymers and macromolecules to proteins, cells, and tissues on up to organ systems. Are all these "parts"—elements, components, subsystems--adaptations? Not according to the current received view: for some part of an organism to be an adaptation, three conditions must be met: first, it must at some time contribute to an organism's ability to survive and reproduce relative to the conditions posed to it by its environment. In this oldest sense of the term, "adaptation" is a relational property that a particular part is said to possess if it helps "fit" the organism to its environment. "Environment" refers to anything outside the organism's "skin": predators, weather, food sources, other members of one's species (conspecifics), and so on. (Vermeij 1987, 23-5) The second condition is that the trait must be common in the population. This requirement insures that the feature's benefits

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aren't merely due to chance. The implication here is that there is some genetic basis, but this need not be known (Vermeij 1987, 7) at least at the outset. (more later). The third condition is that the cause of its commonness be natural selection.[15] (Sober 1993, 84; Sterelny and Griffiths 1999, 217)[16]

It is important to emphasize that "contributing to the reproductive success of an organism" is neither necessary nor sufficient for a trait to be an adaptation. (Sober 1993, 84; Sterelny and Griffiths 1999, 217) The human appendix is often cited as an example of a trait that is the result of natural selection but no longer contributes to our reproductive success (fitness). Among our ancestors, this haven for symbiotic cellulose-chomping bacteria contributed to our fitness, but because of changes in the conditions of our existence (especially diet), it no longer confers any advantage. (Sterelny and Griffiths 1999, 217-8) In other words, this product of natural selection has lost its adaptiveness; thus, it is a "vestigial trait: a relic of previous selection" (218).

On the other hand, just because a trait has adaptive value does not mean that its presence is due to the pressures of natural selection. Two additional conditions must be met. First, in order for selection to favor some feature, there must be heritable variation in the population ("intraspecific variation"). Thus, if a trait is heritable but there is no variation in the population it cannot be deemed an adaptation due to selection. Second,

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[15] In Gould and Vrba's (1982) "adaptation" refers to the process by which a heritable trait that contributes to the fitness of an organism is produced. They use the term "aptation" to refer to the trait itself. (Vermeij 1987, 3-4)

[16] Adaptation, then, is both a process and a state. Indeed, Vermeij, following Gould and Vrba (1982) calls the (selective) *process* "adaptation" since "it generally occurs by the enhancement of some already existing trait." The resulting *state* is an "aptation.". (Vermeij 1987, 13) I shall lay out the terminology that I adopt to address these issues as the chapter proceeds, but, in general, I shall follow Sterelny and Griffiths (1999).

there may be traits that have adaptive value but their presence predates the selective pressure which they currently meet. Thus, "For adaptation, Arnold writes, 'a hypothesis is refuted if the new trait develops before the relevant selective regime.' If the test is passed, it is possible to check whether the new trait really confers an advantage in the new regime that its plesiomorphic [roughly its ancestral] state does not."[17] (cited in Gould 2002, 1235) The question concerning commonly possessed traits that may or may not be adaptive but are not now nor never were due to the action of natural selection quickly brings us to Gould and Lewontin's essay and problems surrounding the adaptationist program.

III.1 Gould and Lewontin's Characterization of the Adaptationist Program

Confusion and controversy concerning adaptation is not merely terminological. For Gould and Lewontin, the key issue is its prevalence. Again, even the simplest of organisms are quite complex—the possession of DNA and the demands of metabolism insure that. Do *all* the parts of these systems contribute to an organism's fitness? Gould and Lewontin claim that much of contemporary research in evolutionary biology operates on the assumption that each part does make a contribution, and that each part has been subject to and shaped by selective pressures. They call this view the "adaptationist program" (AP) (1979)

Gould and Lewontin argue that the AP involves not just conceptual and theoretical claims but also a research program: a scheme which frames and generates

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[17] Plesiomorphic: the original pre-existing member of a pair of homologous characters. The other member of the pair has the evolutionarily novel character which is called the "apomorphic" member of the pair. (Thain and Hickman 1994, 494)

questions and employs an experimental and/or observational set-up for answering such questions. This research program also sets out guidelines for determining what counts as an explanation of the phenomena at hand. There are currently two approaches for discerning adaptations: the experimental modification of the feature in question and the comparative approach. (Vermeij 1987, 3-47) For the most part, Gould and Lewontin focus on the comparative studies associated with, for example, ethology and zoology. (Experimental studies will be addressed in chapters Three and Five.) The following is an example of the AP at work.

The first task for an adaptationist is the identification of the trait, for example, the two-shell (divaricate) pattern found in many molluscs and brachiopods. Next, an investigation in launched into the being's habitat as well as the structure and function of the feature itself. This is done to determine the utility (adaptive value) of this trait relative to the survival and reproductive success of the organism in its environment. Below is an explanation of elements of shell structure relative to the niche of the mollusk *Corculum cardissa.*

> Divaricate ribs may act as scoops or anchors in burrowing which is often done in order to hide from predators. In the remarkable case *of Corculum cardissa* there are mineralization patterns which are translucent while the rest of the shell is opaque. These chevrons are at the rear end of the creature but this oddball actually lays on its substrate with its posterior facing upwards. This works out quite nicely because these translucent chevrons act as windows for endosymbiotic

> algae which dwell beneath them inside of the bivalve. (Gould and Lewontin 1979, 88)

In the above, two morphological features are isolated--the divaricate ribs and the chevron--and the particularity of each trait is shown to increase the fitness of the organism relative to the specific conditions in which it finds itself.

Shells such as the above are classic cases for the adaptationists precisely because of their noncontroversial contribution to reproductive success: they help keep immobile marine creatures from being eaten. Additionally, there is much variation among them, thereby illustrating the way in which selection supposedly shapes a trait to meet the specific demands of varying environments. For example, shells often function as armor. Armor--a hard, unyielding external structure that surrounds softer tissues partly or completely--may function as a passive defense by simply by preventing detection (by smell), or, more familiarly, it may act as a kind of barricade during an attack. But a good adaptationist explanation does not stop there. Some shells protect the organism by making it too big for prey to manipulate or swallow, others are too hard to either break or too well-attached to remove. Thus an investigation into what preys upon these creatures, and what is around and could but does not, may help explain differences in shell size among related species. In general, increased shell size and thickness usually leads to an increase in the fitness, but the manner in which the shell provides defense varies and only by studying the structure of the feature relative to its habitat can the adaptive value be properly understood. (Vermeij 1987, 191-2)

All of the preceding qualities are instrumental in these bivalves' ability to persist and succeed relative to the particular demands in their environ. This requires sensitive attention to the intricacies of the structure relative to the nuances of its niche. In the case of the bivalves, various relations with predators are noted, but other factors such as sediment composition and water temperature may also figure.

Put it in more general philosophical terms, for the AP, form is explained in terms of utility. Utility (adaptive value) is defined as a three-part relation determined by the trait's contribution to the reproductive success of the organism relative to the niche that is occupied.[18] The last aspect of the AP involves the determination of "character evolution": that is, the reconstruction of the evolutionary history of the trait. Such an analysis doesn't stop with the lineage of course, but aims to determine the emergence of the trait as well and the selective pressures that may have preceded that emergence. (Futuyma 1998, 107-8; Gould 2002, 1235)

At its best, the AP is exhaustive in its search to identify the utility of the structure under examination. At its worst, argue Gould and Lewontin, the AP assumes utility far too much, misidentifies traits, and fails to consider alternative explanations. And, more significantly, in both its best and worst forms, it misunderstands what an organism is and overestimates the power of natural selection. Even at its best, the AP's explanatory scope is more limited than it realizes.

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[18] There are, however, two views on how to understand the *functions* of a trait: the etiological theory of functions and the propensity theory (Bigelow and Pargetter 1987). The former is congruent with the definition of adaptation put forward earlier by Sterelny and Griffiths. On this view, the function of a trait is dependent upon its origins (etiology). Thus, on the etiological view, a trait is only an adaptation if it is due to the action of selection. This is the orthodox view, but it is not universally accepted. On the propensity view, the function of a trait is its adaptive effects. (Sterelny and Griffiths 1999, 220-2)

III.2 Panglossian Explanation

One of the aspects of the "The Spandrels of San Marco and the Panglossian Paradigm [...]" that gained it so much notoriety concerned its characterization of the adaptationist program as "Panglossian." Dr. Pangloss—the vulgar Leibnizian of Voltaire's *Candide*—was famous for arguing that every feature of this world we inhabit, however destructive or distasteful, made a necessary contribution to the perfection of this, the best of all possible worlds. In response to Candide's suffering from venereal disease, Pangloss remarked,

> It is indispensable in this best of worlds. For if Columbus, when visiting the West Indies, had not caught this disease, which poisons the source of generation, which frequently even hinders generation, and is clearly opposed to the great end of nature, we should have neither chocolate nor cochineal. (quoted in Gould and Lewontin 1979, 77)

Gould and Lewontin argue that the form of explanation employed by the AP is "truly Panglossian" because it assumes that each trait *optimally* contributes to the overall good of the organism, and, consequently, *must* be as it is. Its first step--isolate a trait and then ask, "what is it good for?"—is driven by the presumption that selection optimizes all features. But what about those cases where the utility of some trait proves empirically questionable? Then, remark Gould and Lewontin, tell another story. For example, when faced with evidence that antlers, horns and tusks are not used as weapons against

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predators, as once presumed, an explanation is offered that claims they figure in intraspecific competition among males. Returning to a shell example, "zig-zag commisures of clams and brachiopods, once widely regarded as devices for strengthening the shell, become sieves for restricting particles above a given size." (Gould and Lewontin 197, 78) In cases where there is morphological variation but no adaptationist explanation, it is assumed that there is some selective pressure active, but it has not yet been identified. It is not that each of these more recent explanations is wrong, say Gould and Lewontin, it is a question of raising the issue of the limitations of the AP to explain each aspect of every living being. (Gould and Lewontin 1979, 78)

The last aspect of the AP that gives Gould and Lewontin concern is one that has special significance for much of the rest of this dissertation. The AP often stresses the utility of some feature in its present context and in the process excludes other attributes of the trait. For example, the short front limbs of *Tyrannosaurus* are so small as to cause one to wonder about what they possibly could have been used for. Perhaps, they enabled the creature to rise from a lying position? They were too short for much else. But, argue Gould and Lewontin, the size of these dainty limbs is more likely to be side-consequence of morphological changes as the head and hindlimbs became larger. (Gould and Lewontin 1979, 78-9)

The purpose of the previous examples is not to show the falsity of the AP *in toto*. Rather, they are meant to illustrate the kinds of questions the AP poses, the assumptions it makes, and the concepts and methodology that drive it. The initial import of the examples is to uncover biases and blind spots. But, Gould and Lewontin are doing more than encouraging self-criticism among fellow evolutionary biologists. They are trying to expose the *conceptual flaws* of adaptationism that lead to improper application.

Gould and Lewontin sometimes imply that, for the AP, the *only obstacle* to optimality for a given organism is natural selection. This supposedly occurs because selection places different and competing demands upon the discrete traits of an organism which leads to "trade-offs" (more details next section)). Gould and Lewontin, however, go a bit too far on this point since the AP does recognize that, at the very least, physical laws place constraints upon selection. The authors generally avoid this kind of overstatement and most of their overall argument does not hinge on it. Our next concern is how their attack on the conception of selection as an optimizer connects to their understanding of the organism.

IV.1 Selection as "Optimizer"; Organisms as Suboptimal "Sets" of Discrete Traits

> The adaptationist program is based on faith in the power of natural selection as an optimizing agent. It proceeds by breaking an organism into unitary traits and proposing an adaptive story for each considered separately. Trade-offs among competing selective demands exert the only brake upon perfection: nonoptimality is thereby rendered as the result of adaptation as well. (Gould and Lewontin 1979, 73)

According to Gould and Lewontin's take on the adaptationist program, selection is considered to be an optimizing agent, and what it aims to optimize are traits (e.g. forelimb length, shell thickness). An important consequence of this view is that, from the perspective of selection—and, likewise, the AP--an organism is a kind of sum of its parts, and this "sum" represents a compromise among competing demands. In the case of *Tyrannosaurus*, the diminution of the forelimbs enabled the increase of head size and hindlimb length and thickness resulting is greater overall optimality—even if the forelimbs in themselves made a lesser contribution relative to the evolution of the lineage and previous ancestral states. This view, as already indicated, presents a number of problems.

As noted above, the AP argues that there are specific features (traits) that contribute to an organism's fitness, and these traits (adaptations) are a result of natural selection. Gould and Lewontin do not deny that adaptations in this sense occur. What they argue is that 1) not all traits are adaptive, 2) all adaptive traits are not the result of selection; 3) what counts as a "trait" is a fundamental problem not sufficiently addressed by the AP. (This also leads to a lack of understanding of the organism as an integrated developmental system.) And 4) the AP encourages unwarranted genocentrism.

IV.2 Criticisms 1 and 2

1/ *Some of an organism's parts do not make a contribution to the fitness of the organism, and 2) selection is not responsible for all the traits that do make such a contribution.*

There are a variety of standpoints that are taken in regard to the phenomena of the adaptedness of organisms and Gould and Lewontin do not clearly distinguish among them. One is called "empirical adaptationism." On this view, adaptation happens, and it is obviously of critical evolutionary significance, but all an organism's features do not make a contribution to its fitness. Godfrey-Smith equates empirical adaptation with a view that selection is of "unique causal importance" in shaping biological structure (Godfrey-Smith 1998, 217), but this view may be tempered somewhat. For example, "neutralists" argue that the conditions in which organisms find themselves are oftentimes not so demanding and many niches are open. (Amundson 1998, 571; see also Gould and Lewontin 1979, 82-5) I noted in my earlier explication of the standard Darwinian view of evolution that the evolutionary significance of differential fitness is directly linked to competition and the scarcity of resources. If conditions aren't all that tough, then many slight differences among organisms will not be as significant. On this view, it is not always "crunch time." As such, many traits do not need to make any significant contribution to reproductive success, nor do they impede it. Or, more technically, there is much nonadaptive variation and many selectively neutral traits.[19] (Amundson 1994, 571; Godfrey-Smith 1998, 717-8)

Another view is that of the "soft adaptationists." This view holds that all traits have adaptive importance, but there are other factors besides selection active in the production of these traits, or, relatedly, impede the action of selection to shape such traits. (Amundson 1994, 572) "Hard adaptationists" argue that "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." (Amundson 1994, 572)

Overlapping the threefold distinction among neutralism, soft adaptationism, and hard adaptationism is the following categorization of adaptationisms put forward by Godfrey-Smith (1998) and further articulated by Sterelny and Griffiths (1999, 227-44).

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[19] For a review of some of the proponents of the neutral theory of molecular evolution such as Kimura (1983) and the related issue of genetic drift, see Futuyma (1998, 320-7).

The first is *empirical* adaptationism of the selectionist variety explained above. The second is *methodological* adaptationism, and the third is *explanatory* adaptationism. The *methodological* version makes no claims about the natural world. (Sterelny and Griffiths 1999, 227) Rather, it holds that the concept of adaptation is useful as an organizing concept in biological *research*. That is, "the best way to study organisms is to look for good design." (Sterelny and Griffiths 1999, 227; more below) Perhaps the most noted purveyor of this view is Maynard Smith who argued that the optimality model discussed above (and below) is a "heuristic device, designed to reveal otherwise unsuspected constraints on adaptation." (cited in Sterelny and Griffiths 1999, 239) Methodological adaptationism, then, is a way of approaching the enormous complexity of living beings relative to the often changing conditions in which they find themselves.

Explanatory adaptationism holds that the mission of biology is to solve the problem of apparent design among living beings. Dawkins, Dennett, (Godfrey-Smith 1998, 717) and Sterelny (Sterelny and Griffiths 1999, 226-7) are noted proponents of this version. They argue that biology's main task is to explain complex adaptation, and it is driven by the assumption that natural selection is the only mechanism capable of producing such design. The unique and overriding power of selection is the central dogma of explanatory, or as Amundson calls it, "hard," adaptationism. Throughout this dissertation, empirical, explanatory, and methodological explanation will be at issue, as will the related issues of soft and hard adaptationism (especially in my Chapter Three, which discusses in detail Maynard Smith and others.)

Sterelny and Griffiths argue that "empirical adaptationism was probably the main target of Gould and Lewontin." (1999, 226) But, in my view, the vitriol fueling the

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debates with Dawkins and Dennett (discussed below and in Chapter Two), among other factors, indicates otherwise. As I shall continue to argue, Gould and Lewontin have taken on the adaptationist *program*. As already noted, their concerns are explicitly in regard to both its concepts (e.g. trait, selection as an optimizer) and its procedures (break the organism into parts, focus on present utility…). Put another way, whether the optimality model constitutes a philosophy of nature, or a methodological heuristic, Gould and Lewontin oppose it. (Gould and Lewontin 1979, 85-9) (The heuristic aspect will further be discussed in chapters Three and Four, by way of Maynard Smith et al. 1985, and Amundson 1998 and others).

IV.3 Criticism 3

3/ What counts as a "trait" is many times not as easily settled as the AP assumes. The AP has a tendency to "atomize" traits. This atomization tends to disregard the parameters of the developmental processes that put these supposedly "unitary" traits together and place them relative to the demands of the functional architecture of the organism. The case of *Tyrannosaurus'* front legs indicates a similar sort of problem.

In his essay "Sociobiology as an Adaptationist Program," Lewontin asks "[w]hat are the "natural" suture lines for evolutionary dynamics? What is the topology of phenotype in evolution? What are the phenotypic units in evolution?" (Lewontin quoted in Dawkins 1982, 37] In the "Spandrels of San Marco […]," the questions are similar but the focus is more upon the notion of what it means to be a "unitary trait."

According to the AP, a trait is a structure optimally designed by selection for its function. Phalanges are for grasping; wings are for flying, ears are part of echolocation devices for locating tiny fast-moving prey, etc. This means that the organism—a bat in this case--is not an "integrated being," as Gould and Lewontin will contend in Chapter Two, but a set of interactions among parts that remain discrete. This

> interaction is acknowledged via the dictum that an organism cannot optimize each part without imposing expenses on others. The notion of trade-off is introduced, and organisms are interpreted as best compromises among competing demands. [...] Any suboptimality of a part is explained as its contribution to the best possible design for the whole. (Gould and Lewontin 1979, 77)

Thus features that do not appear to make a direct contribution to fitness (diminutive front legs) or even those that seem to impede it (some vestigial traits) still play an essential role. That is, the best possible *Tyrannosaurus* has diminutive front legs just as, for Pangloss, if the best possible world has chocolate, then it must have syphilis.

Selection always aims to optimize. As was noted above, adaptation is in this sense a *process*. However, that does not mean that it creates perfect beings, nor perfect parts of beings even from the viewpoint of the AP. Gould and Lewontin do not claim that the AP always assumes the real optimality of the trait under examination, but the optimality model may be used as a starting point or heuristic, ala Maynard Smith's methodological adaptationism. (Sterelny and Griffiths 1999, 239). This is an important point because some defenders of the AP have criticized Gould and Lewontin for attacking a straw man.[20] For example, ardent neo-Darwinian Richard Dawkins (1982)

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[20] Though Gould and Lewontin do insinuate that the AP started off with a perfectionist mindset. That is, the interaction-of-parts view is retained and retrofitted within the

cites as proof the following remark by Lewontin, "[a]daptationism is defined as that 'approach to evolutionary studies which assumes without further proof that all aspects of the morphology, physiology, and behavior of organisms are adaptive optimal solutions to problems' (Lewontin 1979b)." (Dawkins 1982, 30) Dawkins becomes defensive given the suggestion that AP considers nature (selection) to be an optimizer and cites, in defense, one of the purveyors of the program, J. Maynard Smith:

> in testing a model we are *not* testing the general proposition that nature optimizes, but the specific hypotheses about constraints, optimization criteria, and heredity. In the present case we are making a general assumption that nature does not optimize without constraints, and testing particular models of what those constraints might be. (Dawkins 1982, 49)

In the above, contra Godfrey-Smith and Sterelny and Griffiths' categorization, Dawkins invokes a methodological adaptationism—at least in this passage from *The Extended Phenotype*, but not it seems in *The Blind Watchmaker* (for more, see Sterelny and Griffiths 1999, 226-7) Here, Dawkins argues that a restricted version of the "reverse optimality approach" is heuristically valuable precisely because it is a good way to ascertain what the constraints are. (Dawkins 1982, 48, 49) He states, "[t]he animal that results is not the most perfect design conceivable, nor is it merely good enough to scrape by. It is the product of a historical sequence of changes, each one of which is

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adaptationist program after the failure of part-by-part optimization. (Gould and Lewontin 1979, 77) represented, at best, the better of the alternatives that happened to be around at the time." (Dawkins 1982, 46)[21]

Dawkins further elucidates his refined version of the AP with the following point which is meant to distinguish his AP from the follies of Gould and Lewontin's "Panglossian" practitioner who assumes optimality:

> For the Panglossian the demonstration that something is "beneficial" (to whom or to what is often not specified) is a sufficient explanation for its existence. The neo-Darwinian adaptationist, on the other hand, insists upon knowing the exact nature of the *selective* process that has led to the evolution of the putative adaptation. In particular, he insists on precise language about the level at which natural selection is supposed to have acted [my emphasis]. (Dawkins 1982, 51)

But Dawkins' defense against the charge of Panglossianism in no way escapes the main thrust of Gould and Lewontin's criticisms. Indeed, Dawkins' last sentence explicitly states that the AP assumes that selection is responsible and claims that a gene sequence or complex is the unit of the selection.[22] As such, the AP should aim to ascertain the

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[21] (In Chapter Four I discuss arguments against this application of the methodological AP and argue that such an optimization model is not necessary to uncover constraints as Maynard Smith et al., Dawkins, and Dennett (next chapter) suggest. But first all the other issues must be explicated.)

[22] Here, again, the level/unit of selection issue arises. Although this is not a central issue for my dissertation--hence the relegation of these comments to a footnote—it is obviously an important and unavoidable issue as I note in my Intro and partially elaborate upon in CH3, CH5, and CH6. For a good overview of the unit of selection debate relative to many of the issues dealt with in this dissertation, see Sterelny and Griffiths (1999, 53-148; 156-66)

relevant genetic sequences in play and the details of the "selective" history of the trait (e.g. selective regime in place and amount of variation available).

Dawkins admits that the selective history does have (non-selective) constraints, but that does not alter the basic premises of the AP: selection works on traits, the organism is a suboptimal set of these traits, and cumulative selection is the sole force responsible for adaptations. Now Dawkins opts for a "hard" adaptationism in both "empirical" and "explanatory" modes. For example, even in the moderate version of the AP put forward by Dawkins in the *Extended Phenotype* (tempered down from *The Selfish Gene*), the organism is viewed as a suboptimal set of traits.

> For a bird, resources spent on making breast muscles for powering wings are resources that could have been spent on making eggs. An enlarged brain would permit a finer tuning of behaviour to environmental details, past and present, but at the cost of an enlarged head, which means extra weight in the front end of the body, which in turn necessitates a larger tail for aerodynamic stability, which in turn… (Dawkins 1982, 47)

Dawkins sums up his position in the following: "[a]ny view of biological optimization that denies the existence of costs and trade-offs is doomed. And, an adapted/adapting organism is not just a "patchwork of makeshifts' as Pittendrigh told us, it is a tangle of

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As was noted earlier, the AP is often, though not necessarily, genocentric since arguing that the gene is a privileged cause is not equivalent to arguing that selection does not operate at other levels—for example, the individual and/or group. Though Gould and Lewontin don't focus much on the genocentric perspective on the level of selection debate much in (1979), their opposition to the genocentric view is implied in their compromises (Tinbergen 1975)." (Dawkins 1982, 47) I quote these passages at length because the language very effectively transmits the concepts and the method by which the adaptationist program proceeds *according to its own practitioners*, and thus minimizes any charge against Gould and Lewontin that they construct a straw man AP. Now back to the criticisms.

V. The Core of the Dispute: the Integratedness of the Organism, and Looking Ahead to the Development of the Thesis in Later Chapters

Even though Dawkins' slightly reformulated AP does address some of Gould and Lewontin's charges, the latter disagree most strongly with two of Dawkins, and the AP's, central claims: 1) that resources spent on one trait "could have been spent" on another trait. Gould and Lewontin argue that the claim that "resources" can be shifted from powering wings to making eggs within the "animal economy" ignores the specificity of an organism's developmental and structural dynamics, if not the functional, and the processes and structures that they involve.[23] This will be addressed in my Chapters Two and Five.

Relatedly, 2) both "patchwork of makeshifts" and "tangle of compromises" ignore the what Gould and Lewontin call the "integrity" of developmental processes and the primacy of the body plan involved. Issues concerning the latter are most pronounced when seeking to understand not just the production of the structural and functional[24]

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criticism of the AP's tendency to atomize traits (discussed in my previous section). In Chapters Five and Six, I delve into the role of genes in ontogeny in much greater detail.

[23] A functionalist argument against the AP's notion of selection is detailed in Chapter Five drawing upon the works of Schwenk and Wagner.

aspects of traits but also their *arrangement.* The ability of a trait to function is dependent upon its position relative to an ensemble of other parts and functions. And, the functioning of this and other ensembles is then dependent upon the global state of the organism as it develops and attempts to survive. (Gould and Lewontin 1979, 76) Specific cases of the interdependence of parts and traits composing developmental and functional complexes will be discussed in the next chapter and Chapters Five and Six.

A favorite example of both Gould (1977) and Gould and Lewontin (1979) on this issue concerns the human chin. If this feature of the human face is regarded as a trait—a discrete entity able to be selected—"rather than as a product of interaction between two growth fields (alveolar and mandibular), then we are led to an interpretation of its origin (recapitulatory) exactly opposite to the one now generally favored (neotenic)." (1979, 77) Gould argues that we carry no gene sequence for a pointed chin, rather, the chin is a byproduct or side-consequence: it arises because the upper (alveolar) part of the jaw is retarded much more than the lower or basal part. (Gould 1977, 381-2) Thus, although the chin is a consequence of retarded development, it is not a discrete trait, nor is there a gene sequence for it. (The "traits" in this case would roughly be the upper and lower jaw.) As Gould puts it in *Ontogeny and Phylogeny* (1977),

> [w]e are free to speculate about the mechanisms that have brought so many juvenile features into the adult form of our skull. The extreme atomism of "bean-bag" genetics might seek an independent efficient cause for each, tying their coordinated appearance only to adaptive requirements. But I share D'Arcy

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[24] Again, in this dissertation I am dealing mostly with structure and function, not behavior. Hence, my selection of examples from both Dawkins and Lewontin is limited

> Thompson's conviction that complex organic pattern can usually be reduced to fewer and simpler generating [structural and/or developmental] factors. (Gould 1977, 381-2)[25]

We have seen that AP maintains that a trait has its own selective history and an efficient cause that goes with it. Gould argues otherwise: there are many traits, but few efficient causes, the discreteness of many parts is only apparent.

Recall that, for the AP, "discreteness" means that the trait in question makes a distinct and distinguishable contribution to the reproductive success of the population of organisms that possesses it. That is, the trait is discrete in regard to the manner in which it enables an organism to meet some demand posed by the conditions of existence in which it finds itself—thus, feathers enable thermoregulation, hard shells protect from predators, and so on.

However, if Gould and Lewontin are right, then the selective histories for some traits would not be so discrete. This would mean that a fundamental methodological procedure of the AP--isolate the trait, determine its utility, construct a selective history—faces a serious problem, at least in some cases. Yet, an adaptationist might reply—noting the earlier distinction between hard and soft adaptationists—perhaps non-discrete traits exist but they are the exception. But, the opponent to the AP responds, how would the AP determine this? According to Gould and Lewontin, a further methodological problem

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since both are quite interested in behavior.

[25] The passage is followed by a series of citations: "Thompson 1942; Gould and Katz, 1975; Raup, 1966, on generating the range of form of coiled shells with only four parameters; Vermeij, 1973, on the evolutionary significance of "parameterization" I note

for adaptationists is that their approach is in practice unwilling or unable to recognize its limitations. Thus, the nondiscreteness of a trait can be revealed only through an analysis of developmental processes or structural considerations both of which lie outside the scope of the AP which focuses on the trait's relation to selective pressures arising in some given environment.[26]

The nondiscreteness of many traits also leads to a different formulation of the organism. Organisms are integrated entities. Thus, many apparently discrete traits are actually the result of just "a few generating factors" which would involve sets or subsets of developmental processes. Elements of this view were discussed in the Introduction in regard to Newman and Muller and will be laid out in full detail beginning in the next chapter.

Here we see the two perspectives diverge: whereas the AP focuses primarily on the relationship between a trait and external selective pressures, Gould and Lewontin forward a view which focuses on the production of traits relative to internal developmental processes. I call their perspective the "structuralist approach." At this point, the structuralist approach is also *developmental* since it focuses not just on the relation among the forms—Dawkins' "tangle of compromises" version of the AP does that too--but the factors responsible for their generation. For example, in the case of the chin, the key factor is not some selection pressure but what is called "developmental

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all these citations in part because they partially constitute the "developmentalist-structuralist" tradition out of which figures discussed in the following chapters emerge.

[26] More cases of such methodological differences between adaptationist and developmentalist approaches will be discussed in my chapter Four in regard to Amundson (1994).

timing."[27] (Gould 1977, 234-266) As such, in contrast to the AP's focus on selective pressures and the organism as a suboptimal set of discrete traits, we have what will emerge as the "process structuralist" focus on the form-producing processes of development and the integratedness of the organism as a developmental and architectural system. (Sterelny and Griffiths 1999, 26, 51, 231-3, 251) In the next chapter, I shall offer a unique view of how Gould and Lewontin construct an alternative to the AP by constructing a "structuralist approach" and advocating the preliminary version of a paradigm which I will call the "Bauplan Paradigm." As we shall see, however, Gould and Lewontin are not as thoroughly "developmentalist" as their critique of the AP would seem to warrant.

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[27] Here the reader may object, but isn't it at least possible that developmental timing is selected? Though Gould (1977) doesn't think so, inquiry into what are called regulatory genes may warrant such a claim. For present purposes it need only be admitted that this does not alter the significance of Gould and Lewontin's criticism of the atomizing aspect of the AP. That is, an understanding of the processes of development leads to a reformulation of our understanding of how selection operates. It also means that the organism is integrated in such a way that constructing selective histories for discrete traits would be called into serious question. However, it is not at all clear that selection controls developmental timing. This issue will be explored in depth in Chapter Five.

CHAPTER TWO:

STRUCTURALISMS, CONSTRAINTS AND DEVELOPMENT: GOULD AND LEWONTIN'S *BAUPLAN* PARADIGM AND DENNETT'S CHALLENGE

I. Introduction

This chapter continues the criticisms of the AP raised in Chapter One and explores the logic and significance of Gould and Lewontin's "structuralist approach" and their alternative to the adaptationist program, the "*Bauplan* Paradigm" (BP). This is done by focusing upon the different forms of explanation employed by each approach and their respective conceptions of selection, constraint, organism and trait. Gould and Lewontin suggest that the organism is a developmentally and architecturally integrated system. This view constitutes both a critique of the AP and an alternative, though incomplete, approach and model.

In this chapter I argue that there is much insight and innovation in Gould and Lewontin's taxonomy of constraints and their version of what I contend should be categorized as "process structuralism." (However, Gould 2002 is not so easy to label. More in Chapter Six.) Following Sterelny and Griffiths (1999), I define process structuralism as the view that 1) the space of all possible phenotypes (design space) is highly constrained, and 2) many of the organizational features of organisms are explained by intrinsic physical constraints such as those resulting from developmental processes. Gould and Lewontin offer a historicist version of this view.[28] Yet, inconsistencies and inadequacies in their understanding of the relationship between developmental processes

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and adult morphology undermine the viability of their scheme and its purported significance. Ironically, these inconsistencies and inadequacies are most evident in regard to the famous example of the essay, the spandrels of St. Mark's basilica in Venice. However, despite such problems, Gould and Lewontin's approach and paradigm have opened up an important conceptual and methodological space for, at the very least, pointing out critical inadequacies of the adaptationist program in regard to explaining the "deep integration" of developmental processes and macroevolutionary patterns of morphological change and stasis. I conclude by arguing that their most enduring contribution has been to call for non-adaptationist explanations of persistent morphological patterns at the level of development (the phylotypic stage), adult structure (the *Bauplan*), and macroevolution (morphological patterns of stasis and change among metazoans since the Cambrian). Throughout the chapter, I consider adaptationist responses to these structuralist criticisms and of the *Bauplan* paradigm. Of special focus is the "reverse engineering" paradigm developed by Dennett (1995) and Maynard Smith.

I. St. Mark's Spandrels and "The Inversion of Explanation"

Venice's Basilica di San Marco is famous for its engineering triumphs as well as its cross-cultural aesthetic excellence and both make it a seemingly perfect rhetorical object for Gould and Lewontin's philosophical moves. It sports five domes, the largest is near the middle of the basilica, overlaying the space just before the altar area. (It is a "basilica" because it contains a tomb, St. Mark's, behind the altar area.) From an engineering point of view, the place is impressive--constructing sizable domes was a

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[28] Goodwin (1994) and Webster and Goodwin (1996), for example, put forward a related but more ahistoricist formulation of process structuralism.

notable challenge in the 12th century, and, again, St. Mark's possesses not one but five. The site is also known for its marvelous mosaics, as well as the tomb itself and the artifacts stolen from Venice's rival Constantinople exhibited behind the altar area. This Catholic iconography fits wonderfully, perhaps even ***harmoniously***, upon the tapering spaces which rise from the meeting point of the arches (positioned at right angles) towards the bottom of the circular ridge at the base of the dome. Gould and Lewontin define spandrels as "the tapering triangular spaces formed by the intersection of two rounded arches at right angles." Though this definition will cause them some trouble (more below), it is the next claim that sets off the fireworks: the authors claim that these spandrels are "necessary byproducts of mounting a dome on rounded arches" (Gould and Lewontin 1979, 73) resulting from a previous architectural choice to rest each dome on four arches. Before diving into the detail of their structuralist reasoning, first let's consider how the AP might explain such features.

As discussed in the previous chapter, the AP's methodological procedure involves two steps: first, isolate the trait. In this case the "traits" are the tapering triangular spaces. Second, identify their functional role given the local surroundings. The role of the spandrels is to produce a space for the placement for the mosaics: the four rivers of Eden, the four evangelists, the four "acts" of Christ, and so on. In other words, the adaptationist examines the spandrels from the perspective of what they are employed for. For this to be done, the trait or morphological feature is isolated from the rest of the structural system since it is its relation with some environmental demand that is of immediate relevance—whether a maker of mosaics or a marine predator, that is to say, the Holy Roman Catholic and Apostolic Church or natural selection. The apparent "perfect fit" of these depictions upon the surface of the spandrels might lead one to reason that these architectural features are there precisely to provide an, or "the", appropriate place for the various Biblical scenes. This is *iconography* after all. Yet, according to Gould and Lewontin, such an adaptationist account constitutes an "inversion of explanation" (1979, 75). A mistake characteristic of the "Panglossian" aspect of the AP discussed in the last chapter.

For Gould and Lewontin, to explain the existence of St. Mark's spandrels by way of the pictures that adorn it is to employ the same form of explanation as Voltaire's Dr. Pangloss's who claimed that "our noses were made to carry spectacles, so we have spectacles. Legs were clearly intended for breeches, and we wear them." (quoted in Gould and Lewontin 1979, 75) From the perspective of the structuralist approach, however, the question is one of "causation." As such, the proper path of analysis should begin where the "system" begins. That is, from the standpoint of the engineering and architecture of this five-domed basilica, the spandrels are viewed as an "architectural constraint" resulting from the necessity of placing a dome upon four arches. (74) These tapering triangular forms do indeed "provide a space in which the mosaicists worked" (74). But "provide" is ambiguous since, Gould and Lewontin claim, spandrels are an unavoidable consequence of building a structure whose domes are supported by sets of rounded arches meeting at right angles. (86). Such structural, or architectural, necessity is, then, "the reason for their existence." (74, 86) Whatever they are used for besides that—mosaics, dartboards, movie screens—is secondary.

Gould and Lewontin's explanation of this structural feature illustrates what I call a "structuralist approach." The authors argue that the structural system is primary.

Therefore, when it comes to questions concerning the "reason for existence" of some trait, it's place within the structural system—whether basilica or organism--must be considered *first*. Questions concerning the manner in which it is employed are secondary. This is the proper "path of analysis." Gould and Lewontin further argue for this view by way of their construction of a "taxonomy of constraints" (my phrase) and a theory of the organism as an integrated structural and developmental system partially shaped by both historical contingencies and natural selection.

II.1 Introduction to the Structuralist Approach: a Brief History

From start to finish of their essay, the depth of Gould and Lewontin's structuralist approach is striking. Not only does the essay not so coincidentally begin with an architectural discussion of a basilica, it ends with an appeal to the German *Bauplan* tradition and is peppered throughout with favorable remarks and references to D'Arcy Thompson, famous for his geometrical approach to biological development, pattern, and structure in his classic *On Growth and Form* (1942). But the relevance of Thompson's consensus classic is for many not so notable, nor is the *Bauplan* tradition which many argue was appropriately displaced by Darwin. After all, a key move in Darwin's radical break was to explain form genealogically (in regard to commonality of descent) rather than try to uncover some ideal "unity of plan" underlying and regulating biological development and organization. The latter was the structuralist approach that united both Cuvier and Geoffroy Saint-Hilaire--who were otherwise, and famously, quite opposed to one another. (Gilbert 1999, 646-7).[29]

Though there are differing views within it, all 19th century structuralists held that there is a set of principles that both constrain and make possible living beings. This set includes the following: 1) the geometric distribution and functional arrangement of parts that occurs within any given class of organisms is subject to set of principles or "archetype" that make that being/configuration possible--able to survive amidst other living beings in some habitat. The preceding is also the basis for a taxonomy insofar as a

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[29] It his overarching synthesis of many movements and traditions in biology over the last two centuries, Gilbert identifies Geoffroy as a kind of founder of morphology (the search for similarities via underlying principles regarding the production of and relationships among form(s). Cuvier, with his relative stress of differences is identified with comparative anatomy. (1999, 646-70)

particular configuration of components together with certain distinctive characters are what define a class of beings (e.g. the vertebral column of vertebrates). 2) Ontogenetic processes are also subject to these principles: for example, von Baer's law held that developing organisms undergo increasing specialization as they pass from earlier to later embryological stages.[30] The third is perhaps the most notorious for Darwinians.

3) There is a discontinuity among kinds (archetypes). For example, there is no intermediate between vertebrates and arthropods. Relatedly, organisms are not contingent assemblies of parts but beings whose architecture follows a pre-set "rational" plan. The differences between beings of the same kind are just minor variations on a theme (archetype), or, put another way, are variations *within* a kind. The basic components and the arrangement of these components are then preserved despite whatever alterations some particular individual may undergo. (Of course, for Darwin, it is this "undergoing," or inherent generation of variation and subsequent elimination or modification of characters in a population by the conditions of existence, that constitutes the transformative motor of evolution and largely fueled his anti-essentialism.) Thus, as in many essentialist ontologies, the differences between any two given creatures was either small and secondary (of the same kind) or deep and discontinuous (of different kinds).

Structuralists tended to be essentialists for three reasons. First, they argued that there is some invariant feature that distinguishes an organism as a being of a particular kind. Second, change from one kind into another is forbidden and differing kinds are discontinuous. Third, what fixes a being as the kind that it is does not change. For many

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[30] However, not all structuralists were concerned with development.

19th and 20th century structuralists, the distinguishing feature that indicated the essence of some living being was its body plan---sometimes called *Bauplan* or the overtly idealist, nonmaterial "archetype." Again, a body plan is not just a *set* of components, it is the relational arrangement of the set. Depending upon the structuralism, this arrangement might be understood primarily as geometrical, developmental, and/or functional. R. Owen and D. Thompson (1942) emphasized the geometrical, von Baer the developmental, and Cuvier the functional. (Raff 1996, 6-8)

The concept of the body plan was developed and deployed in two distinct intellectual traditions—one involved Geoffroy and Owen, the other von Baer and to a certain extent Cuvier.[31] For Owen, "each group of organisms shares an "archetype," an essential design that underlies the diversity of anatomical detail among the species in the group." (Raff 1996, 33) The ontology here is explicitly Platonic (and decidedly not Aristotlean): the raw material of living beings obtains its form when it "participates in" and is governed by the nonmaterial ideal type. Thus, what was previously identified as a "set of principles" Owen calls an archetype.[32] In contrast with Owen's formal Idealist approach is von Baer's developmental approach which understood the body plan to be

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[31] Von Baer followed Cuvier's view that "organs should be studied functionally as shapes designed for performance, not as ideal series distributed to meet the requirements of philosophical visions." (Gould 1977, 59) Additionally, he followed Cuvier's theoretical framework of the four embranchements, his methodological precept that "science should move from observation to theory, and shun the excesses of unsupported speculation" and, to top it off, wrote a "laudatory" biography of Cuvier. (Gould 1977, 59)

[32] Interestingly, Dawkins chides Darwin for being too much under the influence of Owen's anti-functionalist structuralism. (Dawkins 1982, 31) It is remarks such as these that Gould and Lewontin use to argue that there understanding of structuralism is more anti-neo-Darwinian than anti-Darwin. (Gould and Lewontin 1979, 81-2)

immanent in the ontogeny of each species. (Von Baer's view also has the advantage of not focusing only on the form of the adult.)

Another key structuralist concept—and one of prime significance for Darwin--is homology, developed by both Geoffroy and Owen. In contrast with the functionalist framework of Cuvier, Geoffroy and Owen's morphologically-inclined view focused upon the fact that the same structure or part often performs different functions in different species. The tetrapod limb--a favorite example of Geoffroy, Owen and many contemporary developmentalists and structuralists (more in my Chapters Five and Six)--has the same basic layout whether in a horse, bat, mole, or human even though it is deployed for distinctly different functions: galloping in horses, flying in bats, digging in moles, typing dissertations in humans.[33]

The structuralist tradition also understood many of the complex parts of an organism to be (lower-level) archetypes. As such, there can be archetypes (homologous parts) within archetypes (the body plan characteristic of a group of species). However, the understanding of body plan and homology for all the structuralists, and especially Owen, was idealistic in the Platonic sense. Such Platonism was, of course, driving many of the varieties of essentialism dominant during Darwin's day, and throughout the history of biological thought of course. (Again, it is important not to equate a Platonic idealist essentialism with what might awkwardly be called an Aristotlean teleological essentialism). (Mayr 1982, 38-52; 88-90) What makes structuralism distinct from these

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[33] For Darwin and most contemporary evolutionists, two features are homologous if there is good evidence that they are both derived from, or identical to, some common ancestral feature. As it is now understood, the "features" in question could be anatomical structures, developmental processes, DNA sequences, or behaviors. Again, Darwin

other forms of essentialism, however, is also what makes this tradition so robust for Gould and Lewontin: it is a program which has sought and continues to seek to identify and explain the underlying unity beneath all the diversity. However, for contemporary structuralism to be viable, the idealism must be jettisoned, and it is. Instead of archetypes, Gould and Lewontin rely on the perfectly physicalist notions *Bauplane*, constraints, and the phylotypic stage. Since these notions have been metaphysically reformulated over the past one hundred years or so, the elimination of the idealism has warranted the addition of a new adjective. The term invoked here to name this anti-Idealist neo-structuralist approach is "*process* structuralism."[34] (Sterelny and Griffiths 1999, 228-34, 251) Again, following Sterelny and Griffiths (1999), I define process structuralism as the view that 1) the space of all possible phenotypes (design space) is highly constrained, and 2) many of the organizational features of organisms are explained by intrinsic physical constraints such as those resulting from developmental processes. The *Bauplan* Paradigm is one version of this view.

II.2 Contemporary Structuralism's Version of the *Bauplan*

> the basic body plans of organisms are so *integrated* and so replete with constraints upon adaptation [...] that conventional styles of selective arguments can explain little of interest about them. It does not deny that change, when it occurs, may be

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famously replaced Owen's transcendental "archetype" with the historical "common ancestor." More on this below.

[34] Some structuralism are more developmental, others more "formalist" but the recent trend is more towards the former. The extreme Formalist variety construes the properties of organisms to be physical consequences of their immediate material structure, or embody abstract laws of form as in vertebrates' obedience of the rules of

> mediated by natural selection, but it holds that constraints restrict possible paths and modes of change so strongly that the constraints themselves become [...] the most interesting aspect of evolution. (Gould and Lewontin 1979, 85)

With this passage, Gould and Lewontin's view undergoes a shift. Before, our duo argued that the AP was unable to explain certain aspects of traits or traits themselves and they proposed an alternative approach to explaining such features. In the above, Gould and Lewontin argue that the AP cannot explain the organism-level *ordering* of traits, as well as, perhaps, the existence of particular traits. A body plan is defined by both. For example, vertebrates are defined by the presence of a vertebral column, itself a trait, as well as the number and configuration of limbs—two pairs that exhibit mirror symmetry, etc. Our duo also implies that the entrenchment, or "deep integration," of these configurations (*Bauplane*) is not just a matter of constraints. That is, it is possible that the production of some traits could be constrained but their ordering is not, thus no "deep integration."

The "deep integration thesis" constitutes the "central dogma" of the *Bauplan* Paradigm (BP). In its contemporary sense, a *Bauplan* or "body plan"—I shall use the two terms interchangeably except when noted--is a basic pattern of anatomical organization shared by a group of animals. (Raff 1996, 31) The levels comprising each body plan are hierarchically arranged as "nested sets of anatomical organization. Within each class, orders share a set of characteristics that define membership in that class, and so on to the shared features of species in a genus." (Raff 1996, 30-1) A *Bauplan* is most

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symmetry. Thompson's (1942) is perhaps the paradigmatic work espousing this view. (Gould 2002, 517) often said to occur at the level of phyla, but talk of insect (a class) or whale (an order) bodyplans is not unusual. (Raff 1996, 38)[35]

According to the received view, the "characters used in the delineation of body plans are major features of the overall layout of the adult body or of the developmental trajectory giving rise to that adult body. Relatively superficial characters, such as pigmentation patterns or quantitative variation in size or shape, are *not* useful in this respect." (Arthur 1997, 27) More specifically, a body plan does not refer to behavior or physiology but to major spatio-temporal features of the organism's overall morphological layout. As such, it is defined not by subcellular molecular and genetic levels but by supercellular populations of cells in four-dimensions. (30) Features that distinguish different kinds of body plans include type of skeleton (hydrostatic, internal, external); kind of symmetry (bilateral, radial, asymmetric); number of pairs of appendages (0, 2, 3, 4, many); type of body cavity (acoel, pseudocoel, coelem); cleavage pattern (spiral, radial, syncytial); and the presence of segmentation (unsegmented, segmented).

A classic example of a body plan—and one that helpfully occurs at the level of a phyla--is *Arthropoda*. Arthropods differ in the number of segments (millipedes can have up to 170 segments while arachnids may have as few as 8), the location and structure of appendages (wings, legs, antennae), and the ways in which the segments are grouped into larger units (such as the head, thorax, and abdomen). Yet, a relatively fixed configuration of features underlies all these exhibitions of variety. Most obvious, as the just cited

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[35] However, Arthur (1997) --who along with Hall (1992), puts forward the received view on this still somewhat controversial concept--calls body plans below the level of phyla *Unterbauplane*. (Arthur 1997, 28) Arthur's view is the most developed in this field. In general, it is consistent with the views of Raff (1996), and Gerhart and Kirschner (1999).

diversity illustrates, they are all segmented. Also, all arthropods have a hardened exoskeleton, a ventral nerve cord, a modified coelem, a continuous gut, and three germ layers arise during early development. (Gerhart and Kirschner 1997, 303-4; Raff 1996, 41-2; Margulis and Schwartz 1982, 224-6) These last features and their arrangement are examples of what Gould and Lewontin call the "deep integration" which defines a body plan. And, argue Gould and Lewontin, selection's ability to modify is restricted by the refractory nature of this arrangement. For example, while the number of number of appendages may be varied, the placement of the nerve cord is always on the belly's side of the torso. The authors claim that the source of this integration is due to either phyletic, developmental, and/or architectural constraints.

III.1 Gould and Lewontin's Taxonomy of Constraints

Gould and Lewontin identify three types of constraints: phyletic, developmental (a subset of the former), and architectural. The concept of **phyletic constraints** goes back to Gregory's (1936) distinction between "heritage and habitus." (Gould and Lewontin 1979, 86) Put most simply, organismic morphology is due to two sets of factors: the features inherited from previous generations (ancestry or "heritage") and the manner in which organisms of a particular taxa respond to selective pressures over many generations (the lifestyle adopted or "habitus"). Various historical factors involved in the origination and reproduction of the former not only frame but restrict the ability of selection to shape morphology in order to meet the demands imposed by the latter. They offer the following examples:

I am treating Gould and Lewontin (1979) and Gould (1977, 1989) as incomplete yet largely consistent versions of this received view.

> we acknowledge a kind of phyletic inertia in recognizing, for example, that humans are not optimally designed for upright posture because so much of our *Bauplan* evolved for quadripedal life. We also invoke phyletic constraint in explaining why no mollusks fly in air and no insects are as large as elephants. (Gould and Lewontin 1979, 86)

In his (1980b), Gould explains the prevalence and importance of phyletic constraints via the case of the panda's "thumb" (1980b, see also Sober 1993, 39-40) Pandas are vegetarians and as many know their diet's main course is usually bamboo. In order to strip the bamboo, the animal places the branch between the paw and a small bone that juts out called the radial sesamoid. This bone functions as a "thumb" though it's more bump or stump than full fledged digit. The radial sesamoid's role is normally wrist bone, and in the panda's ancestors it functioned as such. But it has been co-opted. Though the use of the bone is novel, its structure isn't much changed from its nearest ancestors, the bears. Indeed, from a genetic-developmental perspective, no new "digits" have been produced, rather the quasi-thumb arose because of the ossification of a tendon. (Futuyma 1998, 662) Also, from an adaptationist perspective why would bear paws and panda paws be so anatomically similar? Their diets are quite different and so is the way that the each uses its paws, thus the similarity is not due to particularity of present selective pressures but to their persistence as a trait selected for other reasons.

Phyletic constraints like those above (see Gould 1980b and Sober 1993, 39-40 for more examples), also play a critical role in Gould and Lewontin's attack on the AP's claim that selection optimizes. Though the strong sharp teeth of many carnivores and the perfectly sized beaks of Darwin's finches may illustrate natural selection's ability to shape characters so as to form that exquisite fit that both excites and awes, many other traits are not so optimal. The panda's thumb, the human spine, the Orchid's labellum (derived from a simple petal in its ancestor) are not "exquisite contrivances" but awkwardly rigged "contraptions" that would puzzle rather than impress any engineer constructing a machine from scratch for some function. (Gould 1980b, 24-6; Sober 1993, 39)

In sum, phyletic constraints include traits that persist but have lost their original function—cave dwelling salamanders that still possess their useless eyes (Sterelny and Griffiths 1999, 30)—and traits that have been co-opted in less than an optimal way for a new function. Gould and Lewontin call "ontogeny" the cause of this morphological inertia (85)

Developmental constraints (DC's) are those processes or structures that limit the power of selection because of the demands faced by an organism —or one if its particular mechanisms--during the production of phenotype. For Gould and Lewontin, DC's are largely due to the fact that ontogeny is "easily derailed," especially during its early stages when "the differentiation of organ systems and their integration into a functioning body" is taking place. (Gould and Lewontin 1979, 86) Because even minor modifications may interfere with ontogeny, it seems that some change is warded off or "buffered" and rendered ineffectual. (See also CH4-6) Because some mechanisms at some stages tend to resist modification, Gould and Lewontin call them "refractory."

Particular DC's arise because of the structural and/or dynamical aspects all those mechanisms responsible for all those divisions, differentiations, movements, foldings, and transformations that constitute the organismic development. (Described in Intro Chapter II.3 and II.4) Because the form-producing (morphogenetic) processes are tightly integrated, development itself "cannot be pulled apart piece by piece in evolution." (Gould and Lewontin 1979, 86) Integratedness itself, then, leads to constraints on the power of selection since modifications that might increase the adaptive value of some trait but derail ontogeny are not permitted for *developmental* reasons.

Gould and Lewontin go on to make two provocative claims about the evolutionary significance of these constraints in lieu of what they claim is a key aporia of the AP:

> 1) Developmental constraints, a subcategory of phyletic restrictions, may hold the most powerful rein of all over possible evolutionary pathways.
>
> 2) If development occurs in integrated packages and cannot be pulled apart piece by piece in evolution, then the adaptationist program cannot explain the alteration of developmental programs underlying nearly all changes of *Bauplan.* (Gould and Lewontin 1979, 86)

Throughout this dissertation, both of these claims shall receive considerable attention. One of the most enduring and appropriately influential aspects of this essay is how Gould and Lewontin go about linking these two interconnected claims to their developmentalist-structuralist program along with its understanding of constraints and criticisms of the AP.

Indeed, investigating the above two claims has become a chief project in what has emerged over the 1990s as "evolutionary developmental biology." (Arthur 1997, 1-23) In Chapters Five and Six, and to a limited extent Four, this issue will be pursued much further—with relevant recent experimental details—in regard to the work of Arthur (1997) and Schwenk (2001) and Wagner and Schwenk (2000) and the notion of "internal coadaptation, internal selection, and Evolutionary Stable Configurations (ESC's) and the split between evo-devo and devo-evo. But first, on to the other kinds of constraints.

III.2 On the Special Status of Architectural Constraints

> Our own study of organic form, which we call by Goethe's name of Morphology, is but a portion of that wider Science of Form which deals with the forms assumed by matter under all aspects and conditions, and, in a still wider sense, with forms which are theoretically imaginable. (D. Thompson 1942, 1026; quoted in Gould 1971, 67)

The third type of constraints receives the majority of Gould and Lewontin's structuralist attention. These "architectural constraints" are the "necessary consequences of materials and designs selected to build basic *Bauplane*." (Gould and Lewontin 1979, 86) And, they controversially claim, such constraints were never adaptations due to selection. It is here that Gould and Lewontin, but especially the former--see, for example, Gould (1971, 2002)—are most overtly aligned with the structuralist tradition that dates back to the early 19th century. However, again, the authors are careful to distinguish their brand of structuralism from more recent Idealist varieties such as those of Schindewolf (1950), Remane (1971), and Grasse (1977). (Gould and Lewontin 1979, 85-6)

Instead, Gould and Lewontin favor the work of Riedl (1975, 1978) and Seilacher (1972) and focus on the processes of organization characteristic of complex phenomena found throughout the natural world--from hurricanes and galaxy formations to the periodicities generated by the physical chemistry of excitable media (Intro II.3). Some of this work resonates with what is now called complexity or systems theory. (For example, as Sterelny and Griffiths note, "In the language of those new disciplines, highly conserved traits [e.g. homologies] are *strong attractors* for development." (1999, 232)) Riedl's focus is on pattern-formation and self-organizing processes that "find no direct explanation through environmental conditions or adaptive radiation, but exist primarily through universal requirements which can only be expected under the systems conditions of complex organization itself." (Riedl (1987) quoted in Gould and Lewontin 1979, 86) Their utilization of the work of Riedl and especially Seilacher helps complete an at least provisional sketch of their alternative to AP, the *Bauplan* Paradigm (BP).

The work of both Riedl[36] and Seilacher is used to further develop the notion of a type of constraint that is not a consequence of selective pressures (i.e. is phyletic). Again, following Seilacher, architectural restrictions are "the necessary consequences of materials and designs selected to build basic *Bauplane*." (Gould and Lewontin 1979, 86)

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[36] In the spirit of scholarly honesty, two "developmentalists" familiar with my project thought that Riedl deserved much more attention. However, though his *Order in Living Organisms* (1975) contains an innovative and comprehensive structuralist handling of many themes prominent in this dissertation—especially with his notion of developmental "burden"--his work, unfortunately and unfairly, does not figure at all in the literature on constraints or even in evo-devo in general. Integrating him into these debates and the

The key consequence of this is that the basic layout of an organism gives rise to many "necessary byproducts." Some of these are mistakenly considered to be adaptations, as in the previously addressed cases of the human chin (Ch1, Section V.) and St. Mark's spandrels (more below). In the case of the divaricate form of architecture in molluscs and brachiopods, the raised ornamental lines, patterns of coloration, shape of the internal structures and incised grooves are largely due to the properties of calcite as it mineralizes. (87) These "traits," argue Gould and Lewontin, are due neither to the constraints of development nor the demands of selection but arise from the materials employed.

But might these traits contribute to fitness in some way? Gould and Lewontin claim that previous investigation was unable to determine the adaptive value of these "traits" in most cases. (Gould and Lewontin 1979, 87-8) For observational and theoretical reasons, Seilacher replies "no" as well: the colors are not adaptive because they cannot be seen—the bivalves mentioned above either live in buried sediment or are covered with a thick outer layer of cells. Furthermore, the divaricate pattern is "functional" only in exceptional cases and not widely spread in populations—a requirement for selection. (86) In other cases, the divaricate pattern constitutes an architectural constraint which is also a *restriction* on adaptation[37]: "[d]ivaricate ribs may act as scoops and anchors in burrowing (Stanley 1970) but they are not properly arranged for such function in most clams" (88) and are quite "suboptimal." The arrangement of basic features is due to the body plan in play in this phyla. Thus,

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literature is a noble, and lengthy, undertaking cause worthy of pursuit, but a separate project.

[37] Gould and Lewontin do not make a clear distinction between constraint on form and constraint on adaptation as does Amundson (1994, 1998). This issue will be taken up in my Chapter Four.

> [t]he divaricate pattern is a fundamental architectural constraint. Occasionally, since it is there, it is used to beneficial effect. But we cannot understand the pattern or its evolutionary meaning by viewing these infrequent and secondary adaptations as a reason for the pattern itself. (Gould and Lewontin 1979, 88)

Ala Newman and Muller's (2000) cases discussed in the Introduction, the pattern owes it existence to a mix of physico-chemical processes, "some characteristic pattern of inhomogeneity in the *growing* mantle, probably from the generation of interference patterns around regularly spaced centers. [my emphasis]." (87)[38] The problem with the adaptationist program, according to the above, is that by always posing questions about adaptive value, it diverts attention away from explorations into pattern-formation found throughout the non-living natural world that also appear in or employed by organisms. Such processes, argue Seilacher and Gould and Lewontin, explain the fundamental structural aspects of many such traits.

But before we sort through Gould and Lewontin's distinctions and concepts, it is necessary to determine whether architectural constraints might also be a subset of phyletic. The contingency of history is a universally recognized constraint; all organisms have a long line of ancestors and none are perfectly optimal. But is there truly a difference between architectural and developmental constraints? If there is, then the

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[38] Gould and Lewontin also refer to the work of Waddington and Crowe who were interested in pattern formation from the standpoint of embryology, not just selection, though Waddington was very interested in the relationship between genetics (as it was emerging) and embryology as it became, at least partially, developmental genetics. (Raff

example just cited is *not* an architectural constraint since interference patterns generated by a "*growing* mantle" refer to a developmental process. According to Gould and Lewontin, if it is developmental, then it is phyletic and possibly a result of past selective processes. However, as noted in my Intro Chapter, there is a distinction, though often implicit, throughout the literature between physico-chemical processes involved in ontogeny and biologically unique developmental processes (e.g. cellular induction). Our duo, however, is not consistent on the distinction. The reason that the distinction is helpful to their cause is because such the structure and/or dynamics of such epigenetic processes are by definition independent of the action of selection (Intro II.3). As such, these constraints are, from my view, *developmental but not phyletic.* Gould and Lewontin classify them as "architectural" but such a categorization is confusing and even misleading.

In our duo's lingo, developmental and architectural constraints are both active in the production of the deep integration seen among the thirty-five or so body plans that have persisted over the last 500 million years in the animal kingdom. (Sterelny and Griffiths 1999, 287-90) However, I will argue that this failure to maintain the distinction between architectural and developmental constraints indicates an underdeveloped tension in their taxonomy and the *Bauplan* Paradigm. This tension comes to the fore not just in the above misclassification but in the central example of their essay.

1996, 12, 13, 16) Goodwin (1994) develops this line much more than Gould and Lewontin. More on this in my Chapter Four.

IV.1 Spandrels or Pendentives? On Structure, Development, and Dennett's Challenge

Gould and Lewontin made a mistake. They defined a spandrel as a tapering triangular surface that is a necessary byproduct "formed by the intersection of two rounded arches at right angles." (Gould and Lewontin 1979, 73) In fact—in architectural and art history—what they have referred to is a pendentive. (Hersey 1999, 181-2) A spandrel is simply the triangular space between the arch and the flat surface or cornice that lies above it. It need not be *tapering and continuous*. The in-between space may be continuous or punched full of holes, concave or convex, and so on. A spandrel that is concave, continuous and tapering is called a pendentive.[39] Given their definition above, especially with the emphasis on the "tapering triangle," it seems clear that Gould and Lewontin are referring to pendentives.

Does the mistake matter? If one were to substitute "pendentive" wherever Gould and Lewontin wrote "spandrel" does their argument still stand? It does only if pendentives are necessary from the architectural standpoint (as revealed by the structuralist approach) and are not "adaptations." In a critique that is both extended and comprehensive, as well as sarcastic, scathing, and influential (Godfrey-Smith 1998), Dennett (1995) argues that neither spandrels nor pendentives are necessary. For Dennett, our duo's "spandrels"[40] are actually adaptations, not structural necessities. If Dennett is

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[39] Penguin's Dictionary of Architecture and Landscape Architecture (hereafter "A&LA") defines a spandrel: as the triangular space between the side of an arch, the horizontal drawn from the level of its apex, and the vertical of its springing. Such a term is also applied to the surface between two arches in an arcade, and the surface of a vault between adjacent ribs. (Penguin Dictionary of Architecture and Landscape Architecture.

right, then the structuralist approach fails to explain its paradigmatic case! After a brief elucidation of an important architectural point, I will turn to Dennett's formidable challenge and his defense of a somewhat "developmentalist" adaptationist program which he calls the "reverse engineering approach."

IV.2 Pendentives, Spandrels

Gould and Lewontin are right that the space between the arches is a spandrel,[41] though they could have been more precise—and when writing of structural *necessities*, precision is a must. The real question is this: is this kind of spandrel (a pendentive) a necessary byproduct of fixing a dome to the adjoining arches? And, if a pendentive need not be there, must some other kind of spandrel occupy this space or could some other structure fit the bill? Pendentives, like all spandrels, play a role in the support of the dome. (Goodwin, G. 1971, 28)[42] Dennett does not explicitly argue against this (Dennett 1995, 271-3). The conflict concerns the *necessity* of the "triangular tapering" feature. Perhaps, as Dennett suggests, most sympathetic readers of this essay assumed that the kind of necessity being invoked here is "geometric"; that is, is a function of the way in which structures and their geometric properties (size, width, etc.) fit together with other

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[40] For more on Gould's extended sense of "spandrel" and its connection to "exaptation" see Dennett (1995, 273-5), Gould in Selzer (1993 p310-36), and Gould and Vrba. (1981)

[41] A spandrel from the perspective of art/architecture history, not necessarily in their redefined sense (a "nonadaptation") which has some colloquial standing. (Dennett 1995, 268)

[42] Pendentives are characteristic of the Byzantine style/period (Hagia Sophia, Istanbul) and used occasionally in Romanesque architecture (Perigueux), and are also often in the Renaissance, Baroque, and later architecture. Thus, although St. Mark's is a Catholic church, architecturally it has traits associated with the Ottoman tradition. (Goodwin, G. 1971, 28)

structures within a given design. This seems a fair interpretation especially given the references to and Gould's admitted fondness for D'Arcy Thompson and his "geometric" structuralism. (Gould 1971. More below) Such geometric necessity would arise from of an architectural constraint given the blueprint. (For Gould and Lewontin, geometric constraints are a subset of architectural constraints.) Again, they state, "Spandrels *must* exist once a blueprint specifies that a dome shall rest on rounded arches." (86)[43] The assumed consequence of this is that any pendentive "has nothing to do with adaptationist cost-benefit calculation since, there is simply no choice to be made." (Dennett 1995, 271) Dennett takes issue with this charge of "necessity" for at least two reasons.

Gould and Lewontin argue that to properly understand the purpose of the pendentives, one must *not* begin with the mosaics. To do so would be to commit an "inversion of explanation." Gould and Lewontin claim that the mosaics in no significant way impose upon the pendentives, rather, they take advantage of, or "exapt," its properties. (In other words, the properties of the pendentive would be there with or without the mosaics.) Those features that arise for architectural reasons—and have a nonadaptive origin--but later are called on to play an adaptive role are called "exaptations." (Gould and Vrba 1982) For Gould, the notion of "spandrel" and exaptation go hand in hand. (see Dennett 1995, 267-8, 280-1; Gould 2002, 1246-7). Also note that exaptations should not be confused with phyletic constraints since the former had no previous adaptive value.

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[43] From here on out, I shall place quotes around Gould and Lewontin's "spandrels" or simply refer to them as the pendentives that they are.

Dennett's First Criticism: Is "continuous smoothness" a necessary byproduct? As Dennett, and Gould and Lewontin, point out, one of the defining characteristics of these pendentives are their tapering surfaces. Such a feature does not seem "necessary" from the architectural standpoint. That is, building a dome does not require a support structure with a "tapering surface." Not only could the surface be "rough," it could have holes in it.[44] While it is true that the curvature of the pendentive's tapering surface is often "derived" from the curvature of the dome, this is not an architectural requirement, it is an "aesthetic" one. As such, continuous smoothness is not a necessary byproduct but is due to the demands of mosaic construction. Metaphorically speaking, it is an adaptation.

Dennett's Second Criticism: If a dome--a vault of even curvature—is erected on some base, then there "must be" some elements interposed between the supports and the dome. However, Dennett argues, these intermediary components need not be pendentives (or any other kind of spandrel), a squinch[45] would also work. (Dennett 1995, 271-3)

Dennett's second point constitutes a somewhat stronger critique than the first since the pendentives themselves—and not just their smoothness--would fail to count as

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[44] For pictorial illustrations of such possibilities, see Dennett (1995, 271-2).

[45] "A squinch is either an arch or arches of increasing radius projecting one in front of the other, or horizontal arches projecting in the same manner. (*Another* method of developing a dome out of a square is to take the diagonal of the square as the diameter of the dome. In this case the dome starts as if by pendentives, but their curvature is then continued without any break. Such domes are called sail vaults because they resemble a sail with their four corners fixed and the wind blowing into it [my emphasis]." (Fleming et al. 1999, 154))

necessary byproducts of mounting a dome.[46] As such, let's examine Dennett's second, stronger critique first and the case of the squinch.

IV.3 Pendentives OR Squinches?

A squinch is an arch or corbelling system of concentrically wider and gradually projecting arches, placed diagonally at the internal angles of towers to fit a polygonal or round superstructure onto a *square* plan [my emphasis]. (Fleming et al. 1999, 545) In San Marco, the dome is mounted onto a *round* plan. That is the dome itself sits upon a rounded base, not a square or polygonal one. If squinches were chosen, many other changes would have to be made. Furthermore, the continuous surfaces required by the mosaics would have been possible unless some other surface was tacked on over it, an unwieldy and inefficient proposition. So, squinches do not fit the overall scheme of this structure, nor do they serve the needs of the mosaics. Dennett offers no other "actual" (historical) structural options.[47]

This is an important point for Dennett since he argues that not only were there other "imaginable" options to pendentives, but existing ones—in the 12th century. The problem is that he only names squinches and stakes his faith upon a quote from the

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[46] If there was no dome then it just wouldn't be a pendentive. This is not true of a squinch since it can be used for many other non-dome-supporting purposes. This is an important point because a pendentive is a spherical triangle and its curvature is usually that of the dome (whose diameter is the diagonal of the initial square). The triangle (pendentive) is carried to a height which allows the erection of the dome on its top horizontal edge. There are then properties of the pendentive which are dependent upon and interconnected with the dome.

[47] Further innovations could arise that solve the problem of supporting a dome with squinches within such a system, but that begs the question and goes against Dennett's

architectural historian Krautheimer, "Squinches are an element of construction that can be incorporated into almost any kind of architecture." (quoted in Dennett 1995, 273) This is true. They are relatively easy to construct and make very sturdy supports. However, that does not address the major point of Gould and Lewontin. Supporting the dome is not the only issue, it is the integratedness of San Marco's "*Bauplan.*" The replacement of the pendentives with squinches would likely require many other adjustments within St. Mark's: the open space between the columns would decrease as the width of the arches expanded: because of the corbelling process, squinches would require a wider base of support than columns to support ceilings the height of St. Mark's. One might, of course, then change the height, but the same point holds: the design would be markedly altered since the floor plan would be affected and/or possibly the size of the dome. In addition, changes in the width of the arches may affect the size of the dome which could bear upon the materials that could be used, the manner in which the columns could be constructed, the kind of corbelling masonry applied, and so on. Indeed, in the history of architecture, earlier triangular supports eventually gave way to the Byzantine pendentive since the latter could be modified into equilateral and isosceles forms which were better fit for architectural, and sometimes artistic, purposes. Squinches were only rarely employed for precisely these reasons. (Goodwin 1971, 28)

In sum, I think Dennett is right to point out that Gould and Lewontin's "necessary byproduct" terminology is confusing if not misleading. Indeed, as I will discuss in my Chapter Three, "necessity"--and the related notion of constraint—is a tricky term to employ in evolutionary biology. (Also, hinging a difficult and

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understanding of what constitutes biological possibility in the discussion of the spandrels. See especially Dennett (1995, 104-23).

controversial evolutionary argument upon a complicated architectural example may not be so helpful for clarifying tough issues in heated *biological* debates!) However, Dennett fails to deliver the knockout blow he claims to land. (Dennett 1995, 312) Indeed, the failure of Dennett's squinch proposal helps illustrate a key structuralist/BP point: changing one feature sometimes entails making a series of other changes which, at the very least, demonstrates the varying interdependencies of traits. And, for the *Bauplan* Paradigm, it also makes evident the underlying fixity of the body plan itself: complex systems such as organisms are deeply integrated and altering one component may result in changes that undermine or drastically alter the overall structure itself, whether *Bauplan* or basilica.

In addition, the case of the "spandrels" reinforces the notion that the structural system is primary since the configuration of features resists certain kinds of modification to key parts. Analogously, for Gould and Lewontin, selection must work within the parameters set by the body plan. On the *Bauplan* view it is implied that there is a significant number of features that are not subject to selective pressures as are "traits" and "characters" which are by definition "selectable." Some of the features that are not selectable constitute the *Bauplan* while others are minor and as such "invisible" to selection. (Gould 2002, 1258) Returning to St. Mark's, it is structurally necessary--and necessary for the integration and overall function and survival of the structure--for there to be a "spandrel"--that is, some supporting structure connecting the bases of the arches with the dome above. This space may be modified in ways many or few, it may be smoothly tapered or maybe even made of curved blocks, as in Dennett's drawings (1995, 271-2). In this sense Dennett is right, but the alternatives are more "spandrel-like" than he admits since they are going to be rather triangular if not smoothly tapering. The crucial point is that other existing options (the squinches) do not "fit." The constraint, then, is necessary. And even worse perhaps is the fact that all of this back and forth distracts from pursuing explanations as to the how and why of what forms do exist and persist throughout the evolution of various phyla.

IV.4 Returning to the First Criticism: Two Views on the Optimality of Continuous Smooth Surfaces

> The task of reverse engineering in biology is an exercise in figuring out what Mother Nature had in mind. This strategy, known as adaptationism, has been an amazingly powerful method, generating many spectacular leaps of inference that have been confirmed—along with some that have not, of course. (Dennett 1995, 228)

Before we can explore a Dennett-styled response to the Gould and Lewontin defense above, it is necessary to address the seemingly less significant First Criticism: is "continuous smoothness" a "necessary byproduct"? In this section, I argue that Dennett, like Maynard Smith in my Chapter One, accepts elements of Gould and Lewontin's criticisms of the Adaptationist Program. But beyond that, Dennett actually integrates aspects of a "structuralist approach" into his own view. He does this, however, according to the dictates of the AP, thereby producing what he claims is an improved adaptationism and a first glance at what a developmentalist AP might look like. However, a key difference is that Dennett claims Gould and Lewontin overestimate the evolutionary significance of architectural constraints. This leads him to reject the *Bauplan* Paradigm in its entirety. At the end of the section, I question Dennett's conclusion especially in regard to his own understanding of architectural constraints and his conception of natural selection. In turns out that the truth or falsity of the second criticism has significant implications.

To a limited extent, Dennett agrees with Maynard Smith that the "effect of the Gould-Lewontin paper has been considerable, and on the whole welcome. [However,] I doubt many people have stopped trying to tell adaptive stories. Certainly I have not done so myself." (quoted in Dennett 1995, 278) For Dennett, Gould and Lewontin's contribution was to demonstrate the importance of taking structure and development into consideration when trying to understand the reason for the existence of a trait. This means that an adaptationist approach should *not* invoke adaptation when 1) other lower level explanations (as in those from physics) are available (e.g. the tendency of maple leaves to fall down, of why widgets melt in blast furnaces); 2) when the feature is the outcome of some developmental requirement (e.g. that limbs come in pairs, heads are attached to bodies);[48] or 3) when a feature is a byproduct of another adaptation (e.g. a bird's beak's capacity to groom feathers). (Dennett 1995, 247-8) Dennett also grants that "[t]here will always be plenty of undesigned features in a system that is maximally well-designed. (276) That is, although selection is the exclusive designer of adaptations, there will always be many nonadaptive features (277). On all these points, then, Dennett concurs with the *Bauplan* Paradigm but he nowhere goes into the causality of such

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[48] Indeed, even adaptationist comrade Dawkins admits (1989) there are "shapes that certain kinds of embryology seem incapable of growing" (quoted in Dennett 1995, 278)

undesigned "features" nor does he consider their evolutionary significance. On the contrary, he argues that these acknowledgements necessitate no switch to the *Bauplan* Paradigm. Instead he claims that once the "mystical [Idealist] version" of that structuralist paradigm is gone, what is left is *his* view: the "reverse engineering perspective."

Dennett's reformed adaptationism does, in fact, constitute a marked improvement over Gould and Lewontin's "AP" since the former acknowledges that the existence of *architectural* constraints sometimes makes an adaptationist explanation both unnecessary and unwarranted. As such, Dennett accepts Gould and Lewontin's contention that architectural constraints mark a limit for the applicability of AP. However, this reformed AP brings the structuralist approach *within* the adaptationist program by developing what Dennett calls a "reverse engineering" perspective: "good reverse engineering takes the building process into account" (Dennett 1995, 278) Thus the structuralist approach of Gould and Lewontin is *subordinated* to the adaptationist paradigm. The primary reason for this is that natural selection is still regarded as the only designer.

IV.5 Dennett's "Reverse Engineering Perspective" (RE)

So how would Dennett's reformulated AP (hereafter "the reverse engineering perspective" or "RE") explain the relation of spandrels and pendentives to the mosaics, domes, and the basilica itself? From Dennett's perspective, *St. Mark's basilica is structured in various ways in order to properly house and display the mosaics.* Thus, although the smooth surface of the pendentive is an architectural property, its "reason for

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But, they both argue that embryology itself is under the direction of selection. This topic will be pursued at length in my Chapters Three, Four, and especially Five.

existence" is not an architectural constraint. It is, rather, a "design choice." Dennett argues that one of the purposes for building St. Marks was to display the mosaics. Thus, "displaying mosaics" could be considered a "selective pressure" from the perspective of those drawing up the blueprint. Again, from the perspective of "geometry," the smooth surface is not necessary, even from Gould and Lewontin's perspective it seems (more below). As already noted, it could be rough, "non-tapered", perhaps even discontinuous and uneven. (Dennett 1995, 271)

So why "choose" the pendentives; that is, what is the "reason for their existence"? Dennett offers two possibilities: one, as noted above, is that "this smooth surface is ideal for the mounting of mosaic images—and that is why the Basilica of San Marco was built: to provide a showcase for mosaic images."[49] (Dennett 1995, 273-4) This, however, is historically false. In fact, the mosaics were added three hundred years after the basilica was built. Also, all other buildings with domes supported by four arches have spandrels, and many are not ornamented. (Gould 2002, 1256)

Dennett's second reason for the existence of pendentives is more promising: pendentives are close to being the substructure that creates the minimal energy surface

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[49] Interestingly, Dennett sometimes seems to take a kind of holist approach to St. Mark's basilica which is rather Cuvierian since it claims that there is some *function* (displaying mosaics) which is dictates many of the relations among the structures. Gould and Lewontin, on the other hand, stress the importance of a structural feature—the dome—and thus regard the component structures and the relations among the them as subordinate supports. Dennett is clearer than Gould and Lewontin on the issue of the purpose of St. Mark's—why is it built? (see 274)—but, overall, as I suggested earlier, I think that this architectural example in some ways fails to contribute to our understanding of biological form. Oddly enough, Dennett would not agree with me since the RE can be applied to both living beings and human artifacts. My present response to this view—more to will come--is that organisms seem to be generally regarded as structures that aim to survive, reproduce, and modify their surroundings so as to be able to contribute to the

and minimal surface area. In other words, they are an "optimal solution" from the perspective of the AP's cost-benefit analysis. Here we see the reverse engineering perspective in action: first identify and isolate the trait, second assume that there is a good reason for it being the particular way that it is. Third, ask what demands it satisfies given its relationship to other traits within the structure itself—whether organism or church. (Dennett 1995, 273) That is, check is there are nonadaptive reasons for its existence before pursuing the traditional AP (the fourth step).

All this may remind the reader of the AP that Gould and Lewontin so strongly criticized, but there is a difference: the RE seeks *more* than an adaptive story. What it aims to explain is not just traditional fitness as such--what the trait is "for" (e. g. displaying mosaics)--but also the advantages for the other parts and functions when trait X is obtained rather than trait Y or Z. To paraphrase a passage from Dawkins cited earlier, resources spent on wings detract from resources that could be spent on egg laying. Therefore, the "optimal" wings are not just, say, exceptionally aerodynamic, they are those that place the least possible demands on the organism's structure and development. Of special concern are the demands it may place on traits instrumental for traditional fitness: in the avian case, the reproductive system, beaks, eyes, feathers, etc. The RE, then, possesses a two-dimensional notion of adaptive value and recognizes the fitness of a trait from the perspective of its production and structure as well as the function that it fulfills relative to external selective pressures. And, again, Dennett's subordination of the structuralist approach within the adaptationist program is justified by the fact that natural

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fitness of their offspring (and/or adapt). At least some of these qualities would make them nontrivially distinct from basilicas.

selection is an optimizer and the sole "designer," to use Dennett's language, of complex adaptations.

This view, however, is controversial to say the least since the relations among a) cost-benefit analysis, b) adaptation and selection, and c) the structuralist approach are not so easily settled. First off, and contrary to Dennett, just because the pendentive is the minimal energy surface does not mean that it is an adaptation since it may not be subject to selection and/or it may have emerged as a side-consequence of selective pressures on another trait. This is one of the most basic criticisms made of the AP by Gould and Lewontin. However, it must be said that the latter do not fully recognize the implications of this point relative to Dennett's discussion.

Of course, one reason for this is Dennett's book (1995) comes many years after Gould and Lewontin's essay (1979). But the point is that our duo does not allow for the possibility that a concept of optimization may be amenable to the structuralist approach and the *Bauplan* paradigm. This is a mistake. Indeed, the concept "minimal energy surface" directly resonates with the geometric structuralism of Seilacher and D'Arcy Thompson invoked at the end of "The Spandrels of San Marco [...]". Minimal energy surface is not only a concept that does *not* require the action of selection to explain its existence, it is a condition that occurs in the nonorganic natural world as well as in the realm of human engineering. Objects as simple and common as soap bubbles possess such surfaces.[50] That is, based upon Seilacher's perspective as sketched by Gould and

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[50] (Human) engineers have become fascinated with soap bubbles over the past few decades because they can be used to determine what shape--given the constraints of some structure or plan--comes closest to being the minimal energy surface and thus most stable and efficient in terms of the amount of materials necessary for such stability. The significance of this for the present case is that soap bubbles are obviously not forms

Lewontin, surfaces that use the least amount of materials and requires the least amount of energy to be produced may arise as a "necessary consequences of materials and designs selected to build basic *Bauplane*." (Gould and Lewontin 1979, 80). Thus, contrary to Dennett and others, "*Bauplan,*" or at the very least "spandrel" is a necessary concept because it names precisely those forces that fix the fundamental relation of parts. This set of relations is either not subject to selection or modifiable within very narrow parameters. For example, as Dennett himself notes, limb length is modifiable but not the fact that limbs come in pairs (1995, 247-8).

In Chapter One, Gould and Lewontin criticized the AP because it atomized traits and understood selection as an optimizer. However, these two points are not necessarily related. Not only may the AP function without optimization, but optimization might be given a structuralist framework. In a deep sense, this was D'Arcy Thompson's (1942) project. I am not here advocating a return to Thompson, nor are Gould and Lewontin (Gould 2002, 1181-3). Thompson, rather, is a progenitor of the view/approach developed by practitioners such as Seilacher and Riedl as well as Gould. (Gould and Lewontin 1979, 85-9)[51] He states, "Morphology is not only a study of material things and of the forms of

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peculiar to the organic realm, rather they are just one of the many forms available to the production and evolution of organic structures. As in Gould and Lewontin's discussion of Seilacher on the formation of shells, "minimal energy surface" is precisely the kind of quality that merits a structuralist approach, perhaps in conjunction with an adaptationist one. (I explore the possible inextricability of the two approaches in my Chapter Three in the discussion of Maynard Smith et al. and Alberch). Indeed the paradigmatic structuralist, D'Arcy Thompson—who is more "geometric" than developmental--explores the similarity between the ways in which soap bubbles partition with cell division and partitioning within an embryo.(Thompson 1942, 600) (See also Dennett 1995, 273)

[51] It is also worth nothing here that Thompson was an antiselectionist. (Ghiselin 1980, 181)

material things, but it has its dynamical aspect, under which we deal with the interpretations, in terms of force, of the operations of Energy." (Thompson, 1942, 19) In the note which accompanies this sentence, Thompson comes very close to the kind of resource-allocation talk that Dawkins uses, '[t]his is a great theme. Boltzmann, writing in 1886 on the second law of thermodynamics, declared that available energy was the main object at stake in the struggle for existence and the evolution of the world." (1942, 19) For the structuralists--unlike Dawkins, Dennett, and adaptationists in general--what fixes this distribution of energy is not natural selection but the "laws of morphology." Such laws would include, but are not limited to, architectural constraints and *Bauplane*.

A structuralist energetics--or "morphology" in Thompson's sense--may make Gould and Lewontin's approach more appealing since it would become unnecessary to abandon the method of cost-benefit analysis and the concept of resource allocation. Both of these concepts are fundamental in contemporary biology, and, besides, other structuralists such as Goodwin (1994, 53) have employed them in various works.

The Darwinian revolution forwarded a new theory of "natural economy" just as it transformed systematics with its genealogical method. (Ghiselin 1980) The AP and RE develop this Darwinian notion of natural economy—especially in regard to fitness—by way of a biological appropriation of cost-benefit analysis. This adaptationist approach analyzes function and form relative to reproductive fitness given competition and the supposed scarcity of resources in the context of populations as such and individual development (see my Chapter One, especially on Dawkins' version of AP in section IV.) However, just as Dennett's RE appropriated aspects of the structuralist approach in order to produce a more robust adaptationism (e.g. Maynard Smith's rules listed above), it is also possible for a structuralist approach to appropriate cost-benefit analyses within a Thompson-influenced evolutionary morphology. In Thompson's form, this morphology is both geometric and energetic. It is also opposed to atomization, and thus organocentric and holist ("deep integrationist"). As we shall see in Chapters Three and Four, the contemporary views most in line with this particular structuralist approach are found among Alberch and other process structuralists. Next we need to consider the response from the AP/RE, and for that, we return to Dennett and St. Mark's.

IV.6 Biology and Engineering: Dennett and Gould and Lewontin on the Building Process of the *Bauplan*

In his chapter entitled "Biology is Engineering," Dennett (1995) develops the insights of Gould and Lewontin concerning architectural constraints in order to produce a more comprehensive adaptationist perspective, the reverse engineering perspective. Interestingly, in his discussion of the (human) building process, Dennett gives a level of detail not found in Gould and Lewontin. The former points out—this time in regard to English Gothic cathedrals, not Venice's most famous Ottoman-influenced basilica--that "[m]any of the decorative elements of Gothic architecture, such as the elaborate patterns of ribs in the vaults, are really structural functional members—but only during the construction phase." (Dennett 1995, 218) These "ribs" supported the scaffolds necessary for workers to construct the great vaults that formed the ceilings of the cathedrals. After the cathedral was completed, the ribs "became," or were interpreted/employed as, ornamental details. However, their initial reason for existence resulted from the limitations of scaffold strength relative to materials and building techniques in the medieval period. (Dennett 1995, 218) That is, the scaffolds required something to wedge themselves against for their own stability. The ribs and ridges enabled the already built walls to be employed for this function.

From a (non-AP) structuralist approach, these ribs may make better "spandrels" than St. Mark's pendentives although their necessity is perhaps as "developmental" as it is structural. In either case, they are features apt to be misconstrued by the AP since the "reason for their existence" is not to play a role in the "adult anatomy" but are due to construction requirements. As Dennett says,

> The point is simple but casts a long shadow: When you ask functional questions about anything—organism or artifact—you must remember that it has come into its current or final *form by a process that has its own requirements*, and these are exactly as amenable to functional analysis as any features of the end state. No bell rings to mark the end of building and the beginning of functioning (cf. Fodor 1987, p. 103). The requirement that an organism be a going concern at every stage of its life places *iron constraints* on its later features [my emphasis]. (Dennett 1995, 218)

This passage tantalizes for two reasons: 1) Dennett's reverse engineering perspective addresses how the productive process itself places constraints upon the end structure. What of the laborers and their materials and techniques at St. Mark's? Problematically, attention to the actual building process is absent in Gould and Lewontin's discussion. This omission is more than unfortunate, nor should it be shrugged off as an inevitable side-consequence of space limitations. Rather, it indicates a failure to adequately address the *developmental* dimension of the *Bauplan* paradigm. Furthermore, in the passage above, Dennett seems to make development more fundamental than do Gould and Lewontin.[52] 2) The reverse engineering perspective recognizes all these aspects of function as it investigates the multidimensional context of any given trait: from development to structure to traditional adaptive value. As an extensively more comprehensive AP, the RE begins with adaptationist questions, but it proceeds cautiously as it also checks for development and structural forces or effects.

In the end, however, Dennett argues that only natural selection can account for the fact that organisms and their traits are "designed." For Dennett, the distinction of consequence is not between the development of a trait and its adaptive value. It is, rather, between that which is designed (due to selection) and that which is not. Amongst the category "that which is not" are all those features which are due to constraints or contingencies, what Dennett's RE deems "byproducts," "waste," or accidents. (Dennett 1995, 276) Spandrels, as I noted earlier, would also go here. Although Dennett's take on the inextricability of development, function, and adaptation is well-executed, his faith in the power of selection and hard and fast distinction between that which is designed and that which is not are misplaced. (More on this as we proceed.)

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[52] The passage also acknowledges an important development within 20th century biology. The (sub)science of embryology becomes developmental biology because of the recognition that development goes beyond the embryonic stage, that is, it continues in a sense, through adulthood and even senescence. This recognition changes the terrain of functional and evolutionary biology since, as the reference to Fodor indicates, the developmental and functional stages are not merely sequential or so easily separable. It is, of course, arguable whether development emerges as primary. As Dennett suggests, one could construe development as a subset of functional biology as well. This difference isn't so significant for my point here, though it will become so in my Chapters Four thru Six.

Dennett agrees with Gould and Lewontin that constraints are sometimes important because they nontrivially limit the power of selection, but he questions the *evolutionary significance* of such constraints for a number of reasons. 1) Many "constraints" are simply adaptations that have outlived their value but persist for reasons of cost: it's just too "expensive" to change certain ancestral features (Dennett 1995, 279). This represents an "optimizing" explanation Gould and Lewontin's "phyletic" constraints." 2) There are some undesigned features that start off as byproducts of the building process but later obtain adaptive value and then are *preserved* by selection. Using Gould and Vrba's (1981) term, Dennett argues that in this sense all adaptations are exaptations—had either a different use or no use at all--because selection not only lacks foresight, it is completely "blind." (Dennett 1995, 281)[53] 3) Architectural constraints are not significant because they are breakable by selection or trivial in the first place (e.g. limbs come in pairs, heads are attached to bodies).

My initial response is to above is the following. Re: 1): why are some changes more "expensive" than others? Labeling it does not explain it. Also, at what point does an alteration go from expensive to not possible? Or perhaps some features just are not "purchasable"--under the control of selection. Re: 2): Obviously Gould and Lewontin do not deny that some "adaptations" are actually exaptations. The point is that in many other cases, there may not heritable variation for the trait and/or it is not under the control

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[53] One might already recognize a problem with Dennett's view here: does a trait become "designed" if it is selected but originally arose as a byproduct? This is Gould and Lewontin's point: there is a difference between selection's power to preserve a trait and the power to produce ("design") it. This point may be of special prominence if, as Dennett argues, all traits start off as exaptations! More to follow.

of selection. Re: 3): Dennett's third criticism is much trickier, and it is with this third claim that the conflict between the structuralist and adaptationist perspectives becomes most pronounced.

V.1 BP vs. RE

> With *Bauplane* so constrained by phyletic heritage, pathways of development, and general architecture [...] the constraints themselves become more interesting and more important in delimiting pathways of change than the selective force that may mediate change when it occurs. (Gould and Lewontin 1979, 73)

Though Dennett acknowledges the existence of roughly the same taxonomy of constraints—phyletic, developmental, architectural--as Gould and Lewontin, the former has no conception of a *Bauplan*. For Dennett, such a notion takes the conception of developmental and structural constraints too far. Put simply, it is neither necessary nor desirable. For Dennett, the *Bauplan* paradigm errs on three counts: a) it assumes that the received view is incapable of explaining the origination and persistence of bodyplans (thus *Bauplan* as a concept is unnecessary),[54] b) the BP suffers from "physics envy" (Dennett 1995, 227), and c) it is too "internalist." These last two are the undesirable elements. First the internalism.

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[54] As I noted in my Introduction, questions of the emergence and persistence of bodyplans through evolutionary time has been used as a frequent challenge to the received view at least since the days of Goldschmidt's "macromutation" and the continued distinction made by some between micro and macro evolution. (Dennett 1996, 286-91)

For many, the idea that the internal structure and arrangement of parts of an organism is fixed by some set of principles, physico-chemical or otherwise, commits two sins: it is both ahistorical and internalist. It may also be essentialist, a cardinal sin. (See sections II.1 and II.2 above.) For Dennett, and indeed most defenders of adaptationism in its broadest and most inclusive sense, the notion of a *Bauplan* tends to place too much power within the organism. This implies it can direct its own organization as well as its evolution. Such internalism smacks of "orthogenesis" and/or teleology.

V.2 Two Kinds of Process Structuralism: Physico-chemical and Historicist

Gould and Lewontin avoid committing the sins of orthogenesis: they do not argue that an organism directs its evolution, nor do they believe that biology should search for the same kind of (ahistorical) laws supposedly characteristic of physics and chemistry. However, it is the case that the direct action of physical laws on the materials employed by organisms does explain some ontogenetic tendencies and adult structure. For example, calcium is an essential structural element in leaves, bones, teeth, and shells, and plays a variety of key roles in organismic processes such as cell division (Gilbert 1999, 158-9), cell adhesion (92) and the morphogenesis of bones (e.g. ossification) and cytoskeletal structures. (Goodwin 1994, 92-5, 99, 102-5) In its most ahistoricist version, organic form is explained in a manner akin to that of the mineralization of calcite or the various formations that carbon takes as conditions vary (graphite, diamonds, etc.) (Goodwin 1994, 9-11) From this sort of process structuralist perspective, some of the most important features of shells, for example, are due simply to the action of physical chemistry, not natural selection (as Seilacher and Riedl argued above in III.2)

I refer to the above kind of process structuralism as "physico-chemical," or "PC," structuralism.[55] Such a research program draws upon the laws and concepts of abiotic sciences like physics and physical chemistry to construct properly biological laws of morphology and morphogenesis in order to explain key aspects of organismic morphology and its macroevolutionary range. It tends to be strongly ahistoricist and sometimes "externalist"—that is, more interested in biochemistry, morphology and biomechanics than ontogeny. Thompson (1942), of course, is the great patriarch of this lineage and Goodwin (1994) and Webster and Goodwin (1996) are perhaps the best known contemporary expositors of this view, at least in the Anglo-American tradition. Overall, figures within this camp tend to claim that evolutionary biology spends too much time reconstructing morphological genealogies and not enough time explaining (morpho)genesis. (Goodwin 1994, 85-9) Gould sums up this last sentiment in the following illustration of PC structuralism's form of explanation:

> we [PC) structuralists) don't invoke any aspect of history or genealogical connection to explain why Cambrian quartz from Asia exhibits the same crystal structure as Recent quartz from America. So why should we not attribute the logarithmic spirals of Paleozoic and modern gastropods to the same spatiotemporal invariance of physical laws? (2002, 1181)

Gould, however, is not a PC structuralist. For him, although this form of explanation is capable of identifying features independent of selection and explaining their causal origin

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[55] In Chapter Five I examine Schwenk's view (1995) that such laws are actually part of selective pressures. I do not believe such a move works as I detail there.

in a non-adaptationist manner, its scope is severely limited. The reason for its inevitably minor role is due to the fact that the study of the evolution of biological systems is essentially, for Gould, an historical science. (Gould 2002, 1181-2)

As for Gould and Lewontin, the spandrels concept is indicative of their historicist structuralism since the existence of spandrels is always dependent upon selection on other features, and selection is a process both (historically) contingent and irreducibly biological insofar as selection only occurs in populations of complex systems that exhibit heritable variation and possess the ability to be modified to changing circumstances. As Gould states, an "explicitly historical analysis [is] needed to identify the particular foundation for the origin of spandrels in an individual lineage." (Gould 2002, 81) As such, and contra Dennett's jab, Gould and Lewontin, and especially Gould (1980b, 1989, 2002), are far too historically-inclined to suffer from "physics envy." (Dennett 1995, 227) Gould's historicism will be discussed in greater detail at the end of this chapter and in my Chapter Six.

V.3 Internalism

Nor is it the case, contra Dennett again, that Gould and Lewontin believe that some set of "principles" governing the internal organization of biological systems also directs the course of their evolution. However, they are, admittedly, a little bit guilty on this charge and proud of committing at least part of the offence. Though they do suggest that developmental constraints may act as "reins" on evolutionary change, this is not the same as claiming a determined directionality for lineage development, progressive or otherwise.

The structuralist approach, however, does claim that some morphological configurations are inaccessible. There are regions of morphospace—the space of all possible organismic form--that are unoccupied and, say Gould and Lewontin, *they will remain that way*. Even Dawkins agrees with this, he just does not think it's that significant. (Dawkins 1982). More controversially, process structuralists, historicist or PC, argue that some regions of morphospace are "tended towards" or more "attractive" than others. And the reason for such tendencies is not adaptation. This brings us back to the question of the power of selection and, consequently, the explanatory power of the AP. The structuralist perspective claims that when one looks at this evolution of form, selectionist adaptationism is not sufficient to explain what has existed, what exists, and what is possible. More specifically, there are forms that are of high adaptive value which will never be accessed because of the constraints named above. In this sense, constraints are either "positive" or "negative" (Gould 1989, 2002), or "active" or "passive" (Resnik 1995). This is one of a number of claims that leads to the positing and endorsement of *Bauplan* Paradigm. Neither Dennett nor Gould and Lewontin--nor Gould in his other works except for (2002) and (1989) in a taxon-specific manner--deal sufficiently with this debate. It is however, one which I address at great length in Chapters Three and Four (re: morphospace studies) and Five and Six (re: purportedly "positive" constraints")

Again, for Gould and Lewontin, the tight integration of the organism is itself a key constraint on selection. This "refractoriness" is due to all the constraints named above: phyletic heritage, developmental processes, geometrical aspects of structure, the physical *relations* among the forms, and the requirements of functioning itself (e.g.

tetrapods must be able to breathe while they eat and digest[56]) and so on. Dawkins and Dennett grant that physics and chemistry place a range of constraints on what forms can be built, but, the latter argues, given enough time and the power of selection, it is nearly impossible to know what "regions of morphospace" are forbidden. In other words, Dennett's major difficulty with the BP is that, when properly historicized, its central concept (the integrated body plan itself) is not of long term evolutionary significance, especially when one properly understands the algorithmic nature of selection. On the other hand, the BP causally ties together developmental and morphological organizations and therefore macroevolutionary patterns.

VI. Dennett: Selection is an Algorithm

Dennett, like Monod and Jacob (and Gould (1980b!) before him, considers natural selection a "tinkerer" that makes minor modifications with no help of foresight. Given enough time and variation with which to work, all sorts of forms and combinations of form are possible. [57] (Dennett 1995, 226) As was seen above, Dennett grants that this tinkering process is limited in many ways. Of particular salience for Dennett is Kauffman's contribution (1993) which purports to list the rules selection must honor in order to produce adaptive structures. Such restrictions on selection have to do with "the rate at which design innovations can be found, and the order in which design chances can

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[56] Such "functional constraints" will be discussed in Chapter Five.

[57] Gould also calls selection a "tinkerer" but in a much different sense. A tinker is dependent upon what is available. Thus, despite vigorous searching and changing the range of the "given" is outside its power. (Gould 1980b, 26)

accumulate." (Dennett 1995, 223)[58] Also, he acknowledges that at any given time there will be aspects of organismic morphology that are neither adaptations (products of selection) nor adaptive because of developmental and architectural constraints and historical contingencies. Dennett calls these non-adaptive features the "undesigned." (223-7) Yet, in the end, Dennett is well within the version of AP that Gould and Lewontin so strongly criticize.

For example, Gould and Lewontin argue that development proceeds in terms of the differentiation of and elaboration upon interconnected packages, not detachable parts. Thus, one part cannot simply be "tinkered with" without affecting other elements of the organization and its development. This is one sense in which integration itself is a constraint. But for Dennett (and Kauffman), the fact that there is so much inflexibility in the early stages of development is not due to a "canalization mechanism" (a DC) but because "the number of ways to improve organisms by altering early ontogeny has dwindled faster than the number of ways to improve by altering late development." [Kauffman 1993, 77; Dennett 1995, 225. See also Wimsatt (1986)) Yet, here Dennett seems to contradict, or majorly displace, the importance of a point he made earlier. Before, he acknowledged that *there are rules intrinsic to the building process* which constrain selection. Now, he implicitly suggests that selection's "algorithmic" essence (more below) trumps those earlier diagnosed constraints

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[58] Because Kaufmann, however, focuses principally upon the dynamics of the genome and fitness landscapes--and not development and structural constraints--his work (1993) is not of central relevance for my dissertation. However, more will be said on Kauffman's relevance in regard to complex systems theory in connection with Maynard Smith et al. (1985) in my Chapter Three.

Dennett's response to this insufficiently addressed tension is to walk a tightrope between the two sides. Sometimes he argues that constraints are primary or that selection "tinkers" by *complying with constraints.* But, in the end, he gets off on the adaptationist side with his claim that selection trumps the power of constraint, and to some extent the inertia of historical contingency, for at least two reasons. The first concerns the supposed relationship between *Bauplane* and the mode of evolutionary change. Change that results from the accumulation of minor modifications is called "gradual." An alternative view--developed by Gould and Niles Eldredge--is that evolutionary change is marked by periods of rapid change followed by vast stretches of stasis. This is called the "punctuated equilibrium" view of evolution. As Dennett puts it, "Gould's version of the idea is that whole species don't get revised by the piecemeal redesign of the individuals members; species are rather brittle, unchanging things; the shifts in Design Space [morphospace] happen because of species *extinction* and species *birth.*" (Dennett 1995, 297)

The *Bauplan* Paradigm relates to the theory of punctuated equilibrium as follows:

> If new *Bauplane* often arise in an adaptive cascade following the saltational origin of a key feature, then part of the process is sequential and adaptive, and therefore Darwinian; but the initial step is not, since selection does not play a creative role in building the key feature. (Gould 1982a, 383, cited in Dennett 1995, 286)

That is, the key feature is a spandrel due to some architectural or developmental constraint or rule. But Dennett's RE permits that the rate of (still always "small" and "continuous") modifications may change, and that there may be great periods of stasis. He also grants that traits start out as spandrels. His disagreement is over the role of constraints, architectural or otherwise. In Dennett's view, there is no need to invoke architectural constraints to explain the mode of evolutionary change, nor is there a requirement for a concept such as the *Bauplan* to explain the slowness or fastness of change, or its absence. (Dennett 1995, 297-9)[59] The reason for this is that selection is still the only agent capable of producing complex adaptations, and again, being both a (fairly) "hard" and "explanatory" adaptationist, this is what Dennett believes to be the primary mission of evolutionary biology. (CH1, IV.2)

The second reason Dennett argues that selection is primary has to do with its mode of operation. For Dennett, selection is algorithmic, it is "a certain sort of formal process that can be counted on--logically--to yield a certain sort of result whenever it is 'run' or instantiated." (Dennett 1995, 50) A key property of algorithms is that they are "substrate neutral." Therefore, "the power of the procedure is due to its *logical* structure, not the causal powers of the materials used in the instantiation, just so long as those causal powers permit the prescribed steps to be followed exactly." (Dennett 1995, 50-1) An example he uses is all-too-familiar in contemporary evolutionary theory, the running of a computer program: "Electronic circuits are the usual choice, but the power of computers owes nothing (save speed) to the causal peculiarities of electrons darting about on silicon chips. [...And...] the algorithms that will concern us have nothing particular to

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[59] The debate over punctuated equilibrium is far too complicated to be sufficiently addressed by this dissertation. Also, and thankfully, it is not central in the DC's literature nor in the AP/process structuralism debates as I have laid them out. It is worth point out though that defenders of the punctuated equilibrium view need not argue that it is inconsistent with the AP, only that the AP does not explain it. That is, the "received view

do with the number system or other mathematical objects; they are algorithms for sorting, winnowing, and building things." (51-52) From the process structuralist perspective, and using Dennett's lingo, the particular causal powers of development and the morphological materials used in the instantiation of the algorithmic process insure that the "prescribed steps" are NOT followed exactly. Thus, the "sorting, winnowing, and building" are framed, or contorted, by ontogenetic processes and architectural constraints.

Furthermore, it is a bit ironic given his interest in the controversy over punctuated equilibrium that Dennett admits that the "instantiated substrate" does effect the *speed* of the program's operation but then does not consider he implications. The concepts of DC's and *Bauplan* are useful for calling attention to the structure of the substrate and the constraints that affect the rate of change. Dennett, however, claims that the "logic" of the program is not affected by the substrate, nor is it changed by the substrate's speed capacity. Selection's logic is like that of a recipe listing the steps of a process, and it requires "no wise decisions or delicate judgments or intuitions on the part of the recipe-reader. [...] Whatever it is that an algorithm does, it always does it, if it is executed without misstep. An algorithm is a foolproof recipe." (Dennett 1995, 51) And the particularities of the properties of the food and the kitchen do not alter the logic of the abstract process.

When examined under the light of Dennett's conception of selection, the significance of architectural constraints and the rules of the building process fade considerably. The latter are the conditions upon which selection subordinately exercises its logic, mere "substrate." As noted above, occasionally, there will be "forced moves"

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is incomplete [...and...] is silent about that whereof it should speak" (Sterelny and Griffiths 1999, 46-7).

which the tinkerer has to "comply with" but "a tinker who can't find the forced moves is not worth a tinker's damm, and won't design a thing." (Dennett 1995, 226) In sum,

> Kauffman and his colleagues [e.g. Brian Goodwin and other process structuralists] have made an interesting set of discoveries, but the attack on the image of the tinker is to a large extent, I think, misplaced. The tinker, says Levi-Strauss, is willing to be guided by the nature of the material, whereas the engineer wants the material to be perfectly malleable—like the concrete so beloved by the Bauhaus architects. So the tinker is a deep thinker after all, complying with the constraints, not fighting them. The truly wise engineer works *not contra naturam* but *secundum naturam*. (Dennett 1995, 226)

This passage sums up the stark differences between the RE and process structuralism. Again, the latter regards the logic of selection—and the processes of "winnowing, sorting, and building"--to be dependent upon and/or shaped by developmental mechanisms and morphology. And, as I have contended above, the reverse engineering approach's careful consideration of the details of the building process (ontogeny) undermines its conception of selection and the primacy of its power. However, process structuralism must learn from the mistakes and sins of omission committed by Gould and Lewontin's approach and paradigm in order to more fully articulate its mission an a genuine alternative to adaptationism in its various guises.

VII. Conclusion to Chapter Two: A Critical Assessment of Gould and Lewontin's Contributions and My Reconstructing of the Project

It is my view that Gould and Lewontin make four different contributions to the various debates concerning the production and evolution of organismic morphology. They

1) call attention to persistent patterns that merit explanation but are not explained adequately by the AP. These persistent patterns are (adult) body plans, (developmental) phylotypic stages, various constraints on morphology and/or selection (e.g. phyletic, developmental, architectural)[60], and macroevolutionary patterns evinced by paleontology and morphospace studies.

2) construct the foundation for an alternative method to the AP: the structuralist approach

3/ establish the importance of a Taxonomy of Constraints

4/ identify and give a preliminary diagnosis of the evolutionary importance of "spandrels"

In the remainder of this chapter I evaluate the viability and import of each of these contributions. I do this by examining specific issues that are crucial for the debates as

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[60] In this characterization of developmental constraints as patterns rather than processes I am eliding an important distinction. I do this because I do not think Gould and Lewontin are clear enough on this distinction as I argue in the remaining sections. This distinction is further discussed throughout but especially in Chapter Five and Resnik (1995) and Schwenk (1995).

they evolve and for the piecemeal formulation of my own view over the next four chapters. Of particular interest are the relationships among the four.

VII.1 Contributions One and Three: explaining Phyletic Inertia and the Phylotypic Stage

As previously discussed, Gould and Lewontin argue that there are three different categories of constraints: phyletic, developmental, and architectural. Phyletic constraints are features that probably were adaptations but now persist despite their lack of adaptive value. As such, this persistence is not caused by present selective pressures. Gould and Lewontin do not focus much on phyletic constraints as a general category. This makes sense because these kinds of constraints seem to fit with little difficulty within the AP and RE since their existence in no way denies the importance of selection; rather, it indicates that the products of this process can become entrenched thereby posing resistance to future gradual modification.

But what, specifically, causes this "phyletic inertia," and how significant is it for understanding evolutionary change? Gould and Lewontin offer up the following explanation:

> In complex organisms, early stages of ontogeny are remarkable refractory to evolutionary change, presumably because the differentiation of organ systems and their integration into a functioning body is such a delicate process so easily derailed by early errors with accumulating effects. (Gould and Lewontin 1979, 86)

In the above, Gould and Lewontin refer to the developmental dimension of the "deep integration" of organisms. Like Dennett (1995) and Kaufmann (1993), the duo claims that there are stages in development that resist selection since modification risks undermining the ontogenetic system itself; i.e. development is easily derailed.[61] By limiting the modifiability of the component elements of the system, the demands of the ontogeny itself restricts the power and scope of selection. Such "developmental constraints" are among the factors that make organisms the integrated entities that they are. But this view faces an apparent problem.

There is now much evidence that within some phyla the early stages are not so "refractory." (Raff 1996, 208; Gilbert 1997, 900-1) That is, among groups of related species such as salamanders, the earliest ontogenetic stages are divergent. If it were the case that the existence of a phylotypic stage was not nearly as widespread as currently maintained (phyla-wide), the deep integration thesis would suffer a tough blow. However, even in each case where related species exhibit divergence in early development, they still pass through the phylotypic stage which remains highly uniform and conserved throughout the phyla. Thus, although divergence occurs before and/or after this stage, groups of species of the same phyla all pass through a conserved stage. As evolution takes place in a lineage, modifications may occur in regard to various structures, organs, behaviors, colorings, mobility, stability, resistance to desiccation and so on. But that which does not change among the members of a phylum is the embryological stage where the major (and usually adult) body parts are represented in

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[61] This was discussed above and will be dealt with more extensively in Chapter Three relative to Lewontin and Maynard Smith et al.

their final relative anatomical positions as undifferentiated cell groups. (Thain and Hickman, 1994, 484-5; Raff 1996, 208-10, 429) Examples of such stages are the tailbud stage (pharyngula) in vertebrates and the segmented germ band stage in insects.

For Gould and Lewontin's argument to have a chance, what is crucial is not the exact timing of this event, but that it occurs. Evidence of highly-conserved taxon-wide developmental stages illustrates the tight coordination of developmental processes that Gould and Lewontin called "deep integration." It also, they claim, indicates the manner in which developmental constraints restrict the range of modifications open to selection. Further exploration into this channeling or "bottleneck (Raff 1996, 208-10) as an indicator and/or explanation of patterns of macroevolutionary change seems promising. This is especially true since there is already a significant correlation between the phylotypic stage and the adult body plan and evolution is largely the modification of elements of the latter.

However, the structuralist approach as it is applied in regard to the case of the St. Mark's "spandrels" does not invoke the equivalent of such "developmental" constraints and this makes Gould and Lewontin's view, as they lay it out, both incomplete and confusing.

VII.2 Contribution Three and the Relationship between Development and Architectural Constraints

Although dome *building* was one of the great challenges in engineering/architecture in the 12th century, the *building process* is not explicitly invoked in Gould and Lewontin's discussion of spandrels. Because of their focus on the "adult morphology" of St. Mark's, the duo fail to recognize causal agents no longer present after completion (like scaffoldings and so on that are recognized by Dennett in his discussion of the RE and the "ribs." (IV.6)) Adding these elements would give us a different picture of the basilica and a causally richer understanding of the pendentives as they emerged at a particular point after the construction of the arches and the preparation for the base of the dome, and then were "finished" (made smooth) in preparation for the mosaics—most likely after the completion of the dome's external structure (to better shield internal surfaces from the elements).

By failing to address the "developmental" or building process dimension of St. Mark's, Gould and Lewontin add to the confusion over the relationship among the kinds of constraints. Are architectural constraints really a subset of developmental constraints? Gould and Lewontin claim they are not. Following Seilacher (1970), *bautechnischer* or architectural constraints are not phyletic, rather they are "the necessary consequences of materials and designs selected to build basic *Bauplane*." (Gould and Lewontin 1979, 86) Though they were never selected, architectural constraints are the side-consequence of structural changes resulting from selection on traits elsewhere in the organism. (Gould (2002) is much clearer on this as is discussed in Chapter Six.)

The point for now is the following. Given the complexity of even the simplest organisms, it is fairly obvious that modification of one trait will often cause changes, minor or major, to other traits.[62] Thus, as a trait is modified in response to some selective regime—assuming the presence of heritable variation—other traits are impacted in varying degrees. But *ontogenetic* changes are also likely to have side-consequences,

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[62] This would fall under the category of the "undesigned" for Dennett (see section VI. above).

especially during the phylotypic stage when interconnection among the different developmental modules is "tight." (Raff 1996, 205) As such, altered developmental processes are also a source of spandrels insofar as the they produce structures that are (non-selected) side-consequences. This seems consistent with Gould and Lewontin's notion of spandrels as side-consequences. Yet, they fail to note the likely existence of ontogenetic "spandrels" that arise during development. This is particularly true insofar as, for example, alteration of shell width (an adult trait) will involve the modification of a developmental component or mechanism. The alteration of such a major feature's mechanism is likely to impact upon other developmental mechanisms as well as other (adult) traits. (Cases discussed in CH4-6.)

At this point, however, the existence of all the developmental and architectural spandrels may seem paradoxically opposed to the notion of "constraint" insofar as the former involves the emergence of a novel feature. This is a crucial issue because such features may be quite common in any given organism. If this turns out to be the case (Gould 2002, 1247-9), then our conception of development would be profoundly altered from that which restricts selection to that which generates evolutionary novelty. In addition, the relationship between development and selection becomes even more puzzling since as selection focused on the modification of one feature, development would be generating novelty elsewhere. This question is taken up in Chapter Six in the context of Gould (2002), Newman and Muller (2000) and the need for a process structuralism.

The sense in which spandrels are constraints is that such side-consequences cannot be modified without altering the other, presumably selected, feature. This is why

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Gould and Lewontin consider them to be "*necessary* byproducts." In other words, the pendentives must be there, or else no dome. But as has just been demonstrated, ontogenetic elements and processes may also be or contain spandrels. Thus, some developmental constraints, would not be "phyletic"--persistent features that arose probably because of previous selective pressures. If this is the case, and though more needs to be said about it I have no doubts that it is, then DC's should *not* be regarded as a subset of phyletic constraints.

In conclusion, there are at least three problems with Gould and Lewontin's Taxonomy of Constraints. It 1) fails to acknowledge that many developmental constraints may not be phyletic (see above), nor are those that are phyletic explained by the AP (more below); 2) fails to recognize that ontogeny may be a source of spandrels; 3) fails to clearly specify the evolutionary role of spandrels as constraints or novelties. (More on the last two in Chapter Six.)

VII.3 Contribution Two: the Structuralist Method and Non-adaptationist factors that limit Heritable Variation

Gould and Lewontin have given us a method by which to test and further articulate their inadequate and occasionally inaccurate structural approach and *Bauplan* paradigm. In order to explain evolutionary morphology this method instructs us to 1) assess the relative position and structural role of some feature or trait at the level of the adult body plan (e.g. the relationship between wing length, vertebra size, and sternum strength in birds); 2) investigate the elements and dynamics of the mechanism involved in ontogeny of a trait in order to understand its tendencies and the ways it can and cannot be modified. For example, in tetrapod limb formation, the same developmental sequence always occurs: cell condensation, bifurcation, then segmentation. Tripartite branchings never arise. (Sterelny and Griffiths 1999, 233) (This is determined experimentally, see CH5&6)) 3) Determine the degree to which the ontogeny of a trait is interrelated with the development of other traits. This is especially evident during the phylotypic stage when different proto-morphogenetic fields are highly interconnected though their end products might not be. For example, although there is no notable morphological interdependence between the two, heart tissues helps induce the formation of the eye. (Raff 1996, 205)

These three methodological components are critical for two reasons: first, they are necessary for establishing the causal mechanisms for *deep integration*; second, they substantiate the claim that there are developmental aspects that *limit heritable variation* independent of traditional adaptationist concerns: i. e. selective pressures and available genetic variation. "2)" and "3)" are especially critical factors at play in the production of heritable variation. Hence the tetrapod limb details and the possibility that modification of heart tissue may be limited because this would interfere with eye formation. This issue of "internal coadaptation" will be pursued in Chapters Five and Six.

VIII.1 Wrapping Up

It is fairly clear that Gould and Lewontin have given us a version of "*process* structuralism" because there is no adherence to a notion of ideal types (ala Owen and others). Theirs is not a "mystical" version, Dennett's term, of the *Bauplan* Paradigm. But two problems arose for their view. The first concerned the ontological status of "process" in the duo's process structuralism; that is, the relationship between the following two sets of processes, ontogeny and "architecture." While developmentalists must study the role of architectural constraints in *ontogeny*, as well as in the adult, the converse is not the case. Indeed, morphology and biomechanics as research programs can and have gone about their research programs without attending to the intricacies of ontogeny—especially since each is focused on adults. But this divide causes a problem for the *Bauplan* Paradigm. The argument against AP's atomization of parts requires the developmental perspective to justify the "organisms are deeply integrated" thesis. Architectural constraints are undoubtedly restrictions on selection, but they do not sufficiently ground the deep integration thesis. As I have argued, such a view requires a developmental dimension and that is why Gould and Lewontin argue for the refractory nature of early ontogeny.

The second problem concerned the categorization of DC's as phyletic constraints. Phyletic constraints are former adaptations that have lost their original adaptive role. They are likely to have arisen due to selective pressures. To place DC's here is to open the door to selectionist explanations of ontogenetic limitations. But as I argued above, such explanations are not only insufficient, they are misleading.

VIII.2 Postscript: My Reconstruction of Gould and Lewontin (1979) and Gould's Study of *Cerion*'s "Jigsaw Constraint"

There are four flaws in the adaptationist program, even in its reformed RE version, which warrant the construction of a developmentalist and structuralist alternative. Each of these four is a major component of my own view as it is developed over the next four chapters. After each position is stated, the chapter(s) in which it is developed is indicated. These tenets are meant to supplement the core principles of process structuralism as sketched by Sterelny and Griffiths (1999, 26) They are the following:

1) *pointing out* traits that arose due to past selective pressures but now persist beyond their adaptive role neither identifies nor *explains* the origin of the causal mechanisms responsible for this developmental entrenchment ("canalization") and resistance to more recent selective pressures. Only a developmentalist account can explain such entrenchment. Put another way, the AP may explain stage one of the trait, but it cannot explain its post-adaptive persistence (stage 2). This is a major concern in Chapter Three.
2) As I have argued since the Introduction, many developmental processes (e.g. cell adhesion, excitable media) are independent of selection insofar as they are not unique to the biological realm; they are physico-chemical and their properties can be explained without invoking any biological concept or law, including selection. This rules out selective pressures as the reason for the existence of their particular properties. As such, these aspects of ontogeny cannot be phyletic. This is a major concern of Chapters Three thru Six.
3) Selection and genetic variation by themselves do not determine the range of heritable variation. Various developmental mechanisms and aspects do. (Chapter Three, Six)

4) The Deep Integration Thesis is not adequately explained by the AP, nor is macroevolution (Mainly discussed in Chapters Four and Six) For this, a process structuralist approach with an unashamedly internalist focus is required. As Gould puts it, "developmental constraints, with varying degrees of dissociability, both within themselves and one from the other, set the balance between inside and outside in evolutionary biology." (Gould 1989a, 536) See next section.

It would be inadequate and even misleading to present Gould and Lewontin's taxonomy without discussing Gould's oft-cited study on a developmental, and architectural, constraint(s) in the snail *Cerion*. I discuss the case at the end of this chapter because it illustrates all four of the process structuralist posits spelled out in the previous section and because 1) it provides a multidimensional analysis of the causal origin and adaptive effects of a developmental constraint. That is, because *Cerion* does display much variation, both the "positive" (enabling) and "negative" (restricting) senses of constraint are in full view. Also, *Cerion*'s "jig-saw" constraint has both a "formal" and "historical" aspect . 2) The constraint operates upon one of the major features of the snail's body plan, the snail's shell, and has obvious long-term evolutionary significance; 3) the essay is a oft-cited classic study in the developmental constraints and evolutionary morphology literatures.

Cerion is a frequently studied West Indian land snail notable for its "unparalleled morphological diversity." (Gould 1989a, 519) Yet there are ways this snail varies and does not vary due to a set of developmental constraints that are universal to the genus. (Gould and Woodruff 1986). As Gould puts it, "*Cerion* is not malleable putty before a shaping environment." Copious experiments have established this point. (Gould 1989a, 519)

What is constrained is both the development and the morphology of *Cerion* relative to the production of its coiled shell. The shell is a single growing unit, tightly bound by rules of coiling, symmetry, and growth. (Gould 1989a, 520) The shell makes a great case study since all of its ontogeny is embodied in it: the juvenile stages are present in the adult, unaltered, and the exterior of the shell never changes throughout the different stages of development. (520)

Cerion's shell is formed by successive continuous spirals (whorls) and because the adult size of the shell lies within a limited range, an increase in the size of the whorls entails that the number of whorls will decrease. That is, there is a "negative correlation between whorl size and whorl number when adult shells are not free to vary in final size." (Gould 1989a, 520) Gould calls such a constraint "formal" because "this negative interaction expresses no biological principle (beyond the fact that snails coil); it merely reflects the three dimensional geometry of space." (520) The formal character of the constraint is what leads him to name it the "jigsaw constraint" since in a puzzle of a fixed size, the size and number of pieces are also negatively correlated. But the jig-saw constraint is also shaped by a historical factor.

There is more to *Cerion's* development than the relation between whorl size and whorl number. The production of the shell, as is true of almost all species, is allometric: the proportion changes as size changes. This happens twice in *Cerion* which is triphasic:

its initial shape is triangular or button-like, then it becomes more barrel shaped as it gains more in height than width, and it finishes with a slight change in the direction of coiling just before the definitive "lip" emerges. The "jig-saw" constraint only applies to the first two stages.

The restriction upon the morphological variation "that arises from this button to barrel allometry is a contingency of history." (Gould 1989a, 520) It is not a restriction that all coiled beings must abide, neither does it apply to all snails. The jig-saw restriction then is "local" (applies only to *Cerion*) but unbreakably entrenched (it applies to all members within the taxa). Yet, the "doming" aspect of the shell morphology—which is connected to the first two stages, not the last—is the rule among land snails and may apply to marine ones as well. As an architectural feature/strategy, doming works well since it covers more body area with less material. This is true of both Ottoman-styled medieval cathedrals and rapidly growing snails. (Gould 1989a, 520-1) For this reason, Gould suggests that "doming" may be a rule that applies throughout the subphylum *Gastropoda*. (522) This would constitute another developmental constraint, and would be more universal than the jig-saw constraint that applies only to *Cerion*.

So far we have explicated the formal and historical aspects of the jig-saw DC, but only in regard to the manner in which they restrict phenotypic variation. Such restrictions upon development and morphology illustrate the "negative" or limiting sense of a DC. However, there are "positive" senses as well. In its "positive" sense, a constraint "compels" change in some directions rather than others. That is, it is a "channel" for possible future change. The boundaries of this channel are not set by (immediate) selective pressures but by formal and historical factors. (Gould 1989a, 519)

In *Cerion*, the jig-saw constraint (Gould 1989a, 524) insures that variation in whorl size and number remains open despite the fact that the range of adult shell size is fixed—because, perhaps, of adaptive demands relative to predators or temperature. A consequence of the constraint is that changes in width in early ontogeny are correlated with later whorl heights. This is easily seen in large domes, biological or otherwise, since high shell heights require wide bases. Thus, the correlation of these two features is due to a developmental demand, not an adaptive one. Adult shell width, however, is not developmentally constrained and is variable relative to immediate selective pressures, independent of shell height, whorl size and number and so on. (Gould 1989a, 522) That is, shells can be wide and short or tall. Insofar as the variation of dome height entails the variation of early shell width, the jig-saw constraint is a significant factor, along with selection, of the pattern of morphological variation exhibited by the genus *Cerion*. As a general rule, the narrower the range of adult shell size (as is the case with *Cerion*), the more significant the constraint is. (Gould 1989a, 524, 527) Furthermore, because of the overt geometrical restrictions faced by all shelled creatures, *Cerion's* jig-saw constraint gives us insight into why fast-growing snails tend to have shells that are domed. This architectural option makes efficient use of a limited amount of shell-making material by allowing more body to be covered than other architectural options, say a more triangular covering.

In the terminology of Gould and Lewontin (1979), the puzzle-like "jig-saw" restriction is an "architectural" constraint. That is, it applies to all structures. But Gould makes a very curious move when he seems to state that all DC's are composed of both formal and historical factors.

> The major morphological results of the jig-saw constraint are *spandrels* [my emphasis] of developmental channels in the sense of Gould and Lewontin (1979); that is, they are automatic byproducts of *Cerion*'s response to changing whorl size in the context of an unchanged or limited range of adult shell size. Given the universal geometry of filling space in general and triphasic allometry of all *Cerion* in particular, shells with larger whorls will grow fewer whorls to reach a common size, and fewer whorls will yield a squatter shell. (Gould 1989a, 536)

Much more conceptual territory must be covered to fully understand the distinction between negative and positive constraints and the connection of the latter with the controversial notion of "spandrel." (We shall return to these issues and debates in Chapters Five and Six.) But for the purposes of this chapter, I'll conclude with the following point:

> Selection may trigger changes in whorl size, leading to immediate adaptive benefits in width or height, but the consequences outstrip the immediate adaptive value. Also, selection is but one trigger: thus, many triggers' consequence is determined by the jig-saw developmental constraint, not the triggers. (Gould 1989a, 537)

In the next chapter we shall more closely examine the following: the different kinds of constraints and their relationship to selection in the production and modification of organismic morphology.

CHAPTER THREE:

DEVELOPING A "TAXONOMY OF CONSTRAINTS": THE RECEIVED VIEW AND ITS PROBLEMS AND A STRUCTURALIST ALTERNATIVE

I.1 Introduction: Outline of the Chapter

Though the Gould and Lewontin essay (1979) is undoubtedly influential and is still oft-cited as both critique of and/or alternative to the AP, it in no way constitutes the current received view on developmental constraints ("DC's"). That honor belongs to the nine-authored "Developmental Constraints and Evolution" (1985) which I will refer to by its lead pen: Maynard Smith et al. or MS et al.[63] One reason that the "Spandrels of San Marco..." essay is not the definitive article, of course, is that it is more focused upon architectural constraints, despite its proclamation about the possible evolutionary significance of DC's as "reins" governing phylogenetic change. (1979, 86). However, as I suggested in the previous chapter, Gould and Lewontin's taxonomy of constraints is unsatisfactory and crucially confused on the relationship between development and structure. Maynard Smith et al. aim to solve this confusion, and on this *taxonomic* point, I will argue, they are largely successful.

Maynard Smith et al. (1985) have three aims: First, like Gould and Lewontin, the authors attempt a taxonomy of constraints, but they make development fundamental. Thus, rather than distinguishing between architectural and developmental (phyletic)

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[63] Figures as diverse as Dennett (1995), Kauffman (1993), Oyama (1999), Goodwin (1994), Raff (1996), and Dawkins cite Maynard Smith et al 1985 as the definitive article on developmental constraints. The full list of authors is John Maynard Smith, Richard Burian, Stuart Kauffman, Pere Alberch, J. Campbell, Brian Goodwin, R. Lande, D. Raup, and Lewis Wolpert.

constraints, they posit four distinct *sources of DC's*. Second, like Gould and Lewontin, they address methodological issues of practice and offer three procedures for identifying such constraints and (third), four additional means for distinguishing developmental from *selective* constraints. Unlike Gould and Lewontin, and correctly so, Maynard Smith et al. do not consider developmental constraints to be necessarily "phyletic" (due to the past activity of selection). Instead, they explore the relationship between developmental processes and selection noting that, depending on the case, a constraint may be due to the action of either of them, while in others, *both* are active in the production of a single developmental constraint.

I will argue that Maynard Smith et al.'s taxonomy is an improvement over the figures addressed thus far, because it more fully integrates developmental biology. However, though there is greater clarity and explanatory success in their sketch of the different *kinds* of DC's, the question of the evolutionary *significance* of these various kinds is not sufficiently addressed, especially because of their overriding selectionist bias, as they admit. This, I argue, is unsatisfactory. Because of the insufficiency of their account, I draw upon the additional work of co-author Alberch who, I argue, offers an alternate view for solving the ambiguities somewhat conceded to by Maynard Smith et al. What is at stake in this debate is the not only the explanation of morphological production, modification, and innovation relative to the role of selection, but, as in Gould and Lewontin (1979), our understanding of evolutionary stasis and change, as well as the conception of the organism itself.

I.2 From Gould and Lewontin to Maynard Smith et al.

For Gould and Lewontin, a developmental constraint is a subset of phyletic constraints. As was discussed in my Chapters One and Two, phyletic constraints are due to the accidents of history, and it is often the case that they are the result of selective pressures no longer present. Architectural constraints are not developmental ones, nor do they fall under the heading phyletic. Such *bautechnischer* are causally separable from the history of life; they are nonbiological in origin. (A *Bauplan* may actually be made of both kinds of constraints, though Gould and Lewontin often aren't clear enough on this point.) Maynard Smith et al. adopt a different scheme and argue that "architectural" constraints are a subset of developmental constraints.

MS et al. define a developmental constraint as "a bias on the production of variant phenotypes or limitations on phenotypic variability caused by the structure, character, composition, or dynamics of the developmental system." (1985, 266) In recent works by Goodwin (1994), Webster and Goodwin (1996), Sterelny and Griffiths (1999), Dennett (1995), Amundson (1994), Resnik (1995) and Raff (1996), this is the definition from which each view begins and largely stays within. Yet, the apparent commonality among such diverse figures is puzzling. How could opponents agree on such a controversial issue? A few possibilities emerge. First, one's view on DC's actually does not matter much since most key debates over macroevolutionary stasis and change are independent of it. Thus, views *A* and *B* may agree on this definition of DC's but continue to disagree on key related issues—for example, on the integratedness of *Bauplane*. Second, the definition is so minimal and/or indeterminate-underdetermined that no one bothers to reject it. As such, both *A* and *B* are able to appropriate and modify it to suit their conflicting aims. Indeed, the usage of the term "bias" might promote such indeterminacy. Third, either *A* or *B*'s agreement with the definition is inappropriate. That is, *A*'s adoption of the definition leads to inconsistencies within the views of *A* on other issues.

Whereas all three possibilities were entertained in the previous two chapters, Maynard Smith et al. reject the first outright. According to their view --and most of the authors just listed--it is clear that DC's "undoubtedly play a significant role in evolution. Yet there is little agreement on their importance as compared with selection, drift, and other such factors shaping evolutionary history." (1985, 265) As the essay proceeds, they seek answers to the following questions: 1) how do DC's arise in evolution? 2) How can we recognize them? 3) How can their effects be distinguished from those of selection? And, 4) how, if at all, do DC's affect the future evolution of morphology? It is my view that the great differences among the co-authors illustrates the extensive malleability of the definition rather than some underlying commonality. This malleability leads to a key inadequacy in regard to Maynard Smith et al.'s ability to assess the evolutionary significance of developmental constraints. However, an alternate view can be developed by drawing upon two sections of the essay and the independent work of one of its more notable co-authors, Per Alberch.

II. The Production of Developmental Constraints

According to Maynard Smith et al. (1985), there are four ways in which developmental constraints may arise. The first (hereafter MS#1) is due to the properties of the materials out of which organisms are built and the invariant laws of physics. (266) An example they offer is the law of the lever: "any uncompensated change in the shape of a skeleton that increases the speed with which some member can be moved will reduce the force with which that member can exert." (267) In cases where this first constraint is operative, invoking historical contingencies or past selective pressures is unnecessary. Put another way, the organism's feature is an instantiation of a law, and the manner in which the law applies is not unique to biological phenomena or evolutionary history. These constraints are universal in the sense that they apply to all physical systems and/or to all things built out of the given materials (Maynard Smith et al. 1985, 267)—whether biological or geological, a simple tool or a sophisticated technological system.

The second constraint (MS#2) is closely related to the first. It is also due to a source which shapes nonbiological phenomena as well, but the set of such phenomena is much smaller: these are the laws said to govern complex systems. Not all complex systems are organisms, of course, but all organisms are complex systems. In the most minimal sense, a system is complex if the units composing it interact in a way that conflicts with randomness. (Sole and Goodwin 2000, 42-3) (More on complexity below.) Examples of these phenomena involve an organism's temporal and spatial properties and

> include point stability, limit cycles, and propagating waves. These capture the dynamical essence of a number of biological properties such as homeostasis, excitability, oscillations (with phase-setting, phase-locking, and annihilation properties), such as circadian rhythms and heartbeat [...] and wave propagation (such as occurs in nerve impulse conduction and in such morphogenetic movements as gastrulation and neurulation). (Maynard Smith et al. 1985, 268).

Cell sheet folding (invagination and evagination), the formation of an animal's basic cell layers (gastrulation), brain and nervous system (neurulation), and other organs (morphogenetic movements) are or involve complex systems. This means that there is a set of developmental—and functional (e.g. homeostasis)--constraints that are due to the "construction rules" in play in the production of complex systems. (More in Ch. 5 and 6) Here, Maynard Smith et al. place what Gould and Lewontin called the "architectural" within the developmental. Since the organism is itself a complex system—as is widely acknowledged—and since such systems are especially important in development, Maynard Smith's move seems not only justified but noncontroversial at this point (it was perhaps more controversial in the 1980s). Indeed, in many of their writings, Gould and Lewontin emphasize the significance of the fact that organisms are complex systems, but they are not as consistent in their emphasis of the importance of development.[64] A different, and "more speculative," point about complex systems concerns what Stuart Kauffman has called "the branching effect."

Another example of the relevance of complex systems to evolution concerns the rules governing the production of cell types. There is no common ancestral cell or cell type from which any given cell type could be derived. Rather, one cell type can only give rise to a small number of others, usually one or two: "In this respect, development follows a branching pathway." (Maynard Smith et al. 1985, 268) Thus, at any given point in cell development--and consequently in tissue and organ formation--the

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[64] For more on the contingency of development relative to Gould, see Oyama's "The Accidental Chordate." (Oyama 2000) The story is slightly different for Lewontin (see especially Levins and Lewontin 1985), though this difference is not relevant here and is outside of the scope of this dissertation.

transformation of cell types is restricted.[65] "Branching" then is the phenomena wherein from any given stage, only a few possible transformations (e.g. 2) may occur, though taken together, the number of possible stable states is more than a hundred. (Maynard Smith et al. 1985, 268)

The third constraint (MS#3) concerns the storage and retrieval of information during development (see also Kauffman (1993, 173-236, 411-520); Dennett (1995, 107-23); and Raff (1996)). The point is that genes are not autonomous agents floating in a vat but are parts of a (genetic) system that has its own dynamics and rules and "various features of the genetic system affect the likelihood of a lineage producing "favorable" novel genotypes, and hence phenotypes." (Maynard Smith et al. 1985, 271) In other words, the "bias" ascribed to DC's in the beginning of this section (in the definition of DC) "may also result from biased *variation in the genetic mechanism itself* [emphasis in the original]." (282) This is distinct from forces or phenomena which act *on* the genetic system such as those "enzyme pathways that modify the structure of a gene in direct response to specific relevant stimuli from the environment (Campbell 1982), so permitting what Echols (1981) calls "inducible evolution."" (Maynard Smith et al. 1985, 283) It would seem that the action of these enzyme pathways is not a DC in any usual sense of the term—is induction a "bias?"--but the constraints operative within genetic systems are characterized that way by MS et al., though not consistently. This is

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[65] Also, the ability or "competence" of a cell to respond to an inducer--and then divide, migrate, change shape, and/or differentiate--is time and space-dependent during development. (Futuyma 1998, 53) Thus, just as types of cells can only be transformed into a small subset of other cell types, cells face certain restrictions due to their developmental context in both time and spatial position (relative to other cells, tissues, etc.) As such, cell competence is one element that both constrains and makes possible transformation during development. More on this dual sense of a restriction that both constraints and enables as we proceed.

important because the genetic level has been and oftentimes continues to be characterized as an abstract "unit of selection" when it is more accurately understood as a system with its own dynamic. (see especially Kauffman 1993) Furthermore, if genes and the genetic system are considered to be part of the developmental system, then selection is not the only force acting on this level since genetic systems are subject to, and constrained by, various levels of dynamical (e.g. functional, structural, developmental) constraints. (Maynard Smith et al. 1985, 266) That is, as argued in my Intro and later in this chapter, development is "hierarchical."

The fourth constraint (MS#4) is the one most often directly associated with ontogeny. These are the "particular features of the evolutionarily determined pathways of development examplified [sic] by a group of organisms" (Maynard Smith et al. 1985, 266) Sometimes called "canalization" or generative entrenchment" (Wimsatt 2001), these constraints are due to the ontogenetic processes themselves—such as the morphogenetic movements noted in the Intro and Chapter Two. These are the processes that give groups of organisms their most distinguishing traits such as the tetrapod limb found in all vertebrates or the whorls of *Acetabularia*. (Goodwin 1994, 77-114) MS#3 is not nearly as relevant for this dissertation as MS#4 unless it could be argued that, in an inversion of Dawkins (1982)[66], the storage and retrieval of information (i.e. patterns of gene expression etc.)) is constrained by ontogenetic mechanisms (MS#4), and is not just a restraint on selection. Again, sometimes Maynard Smith et al. argue this way,

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[66] Dawkins has argued that the developmental systems are subordinate to the genetic system and thus to natural selection (thus his genocentrism in terms of the unit of selection.) (Dawkins 1989, 62)

othertimes they don't.[67] Another possible view is that the constraints arising from the genetic system is a complex system feature (MS#2) and not a classic DC (MS#4). In any case, this is not a central issue for my dissertation largely because my focus is on development and morphology, and MS#3 is less significant for such a focus than MS#1, 2 and 4.

The point of the preceding speculations is that while MS et al. identify four causes of DC's, there is oftentimes a search for the causes of those causes, or the controller of them. For adaptationists, this search is often driven by the belief that complex organismic features must arise due to selective pressures (CH1, IV.2). I shall argue below that MS et al. wrongly lapse into this adaptationist position where development is largely subordinated to various modes of selection. There are many reasons for the failure of such selectionist views, but again, one already noted is that even if some DC's were due to past selective pressures, their persistence is due to developmental factors and not selection, by definition! Also, the relationship between DC's and complex systems remains unresolved. Much of the rest of the essay is a meditation on the many dimensions to MS#4. In the next section, I continue with Maynard Smith et al. before moving on to the problems that arise, and Alberch's ignored alternative view.

III.1 The Scope and Bindingness of Particular Developmental Constraints

The next distinction of importance for MS et al. concerns an issue which arises in the above but is not clearly spelled out: the taxonomic scope of a given DC and its degree

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[67] This tension or wavering may be due to Kauffman (1993) who originally argued that complex systems theory demonstrated Darwinism's intrinsic inadequacies. However, as Dennett points out, Kauffman now seems to argue that his view can be integrated into the AP—as Dennett does in his reverse engineering approach. (Dennett 1995, 220-8)

of entrenchment or "bindingness." DC's differ in taxonomic scope: some are more extensive or "universal" and apply to entire phyla or even the animal kingdom as a whole, others are more "local" and apply only to subphyla or classes.

All universal constraints are constraints MS#1: i.e. due to the laws of physics and/or the properties of materials. There seem to be no other universal constraints besides these, which, again, apply not just to all organisms but to all physical systems. In contrast, local constraints are confined to particular taxa and "arise in consequence of some particular feature of the organisms of those taxa." (Maynard Smith et al. 1985, 267) "Local" and "universal," the authors contend, mark the ends of a continuum and are not intended to be logical contraries.

There are two logically independent criteria for judging universality: the scope and "bindingness" or "entrenchment." For example, the amino acids comprising the proteins of all existing species are made up of L- rather than D-isomers. However, even if this fact proves universal in *scope*, its *bindingness* is less clear, especially since early in the history of life, both L- and D- isomers were present in amino acids. Put another way, the fact that the proteins found in all extant species are made up of amino acids with L-isomers is not a law of physics, nor is it due to a restriction placed upon organisms by the properties of the materials in question. In this case, the constraint seems to be historically contingent (Gould and Lewontin's "phyletic" though not necessarily because of selective pressures). Initially this property was not fixed, but it developed into a pervasive constraint though it "plays an ill-understood role in the development of all terrestrial organisms." (Maynard Smith et al. 1985, 267) This seems to be the case in regard to life's employment of DNA--and chitin (a nitrogenous polysaccharide employed for its

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structural rigidity and chemical resistance) as well. In either case, a constraint arises from the fact that certain groups of organisms are "locked into" using particular materials, but this may change through time. (268) Both of these points are very friendly to the historicist side of Gould insofar as it illustrates the significance of contingency itself as a constraint in regard to structure and function in a way that is independent of both selection and developmental constraints. Interestingly, Dennett too has a fondness for these kind of cases since, he argues, many developmental constraints are actually historical contingencies, not insuperable barriers (or guides) of selection. (Dennett 1995, 277-9)

The difficulty of distinguishing local from global constraints and determining the importance each plays in evolution is nicely illustrated by the authors' example of palms. Palms are monocotyledons; they possess trunks relatively uniform in diameter that do not branch. Dicotyledons posses the capacity of secondary thickening, thus their trunks are able to taper and branch. As such, "[t]o the extent that secondary thickening is not available, the ways in which monocotyledons can grow and the structures that they can achieve are constrained." (Maynard Smith et al. 1985, 267) But, as it turns out, there are palm trees that branch! While for some, like Dennett, this would seem to suggest that constraints are not that significant, Maynard Smith et al. disagree. First, just because a constraint is "breakable" does not mean that it is not a constraint.[68] This is even true of

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[68] The breakability of a constraint is also used, by Dennett and others, against the *Bauplan* position. In still other cases it is used to argue that the constraint is not influential because it can be overridden, presumably by selection. In many of these cases, what is implicitly argued is that either selection is guiding development--and subsequently the DC 's that emerge and persist--or it is claimed that selection is not causally influencing development as such, but it retroactively approves or disapproves of the existence of a DC. In the next section, I will explicate Maynard Smith et al. position

"local" taxon-specific constraints. Second, the fact that a constraint was overridden does not mean that it has had no significant effect on the pathways followed by evolution (or future paths). On the contrary, *"[b]y biasing the likelihood of entering into one pathway rather than another, a developmental constraint can affect the evolutionary outcome even when it does not strictly preclude an alternative outcome* ([my emphasis]." (Maynard Smith et al. 1985, 269)

III.2 The Significance and Role of "Biases"

The fact that constraints are not absolute prohibitions diminishes their significance no more than genetic drift's "overriding" of selection diminishes its significance. Local constraints are "biases," and Maynard Smith et al. (1985) argue that such biasing "is more consistent with the diversity and unpredictability of evolution than is the setting of absolute prohibitions." (269) Much of the rest of their essay develops the discussion of the sources of these constraints and the degree to which they affect the production or "accessibility" of phenotypes given a particular developmental mechanism, ontogeny in general, and selection.

Every developmental mechanism is biased in two related senses. First, a developmental mechanism, as a mode of (phenotypic) production, tends towards a certain sequence of states rather than others. Some states are avoided for reasons of instability, others are inaccessible because of the rules, however modifiable, that govern the production process (e.g. cell type, number, and size). In general, it is the persistence, and reproduction, of *regularities* that make the construction of some trait possible. A

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on the nature and importance of local constraints and the implications for evolutionary theory.

consequence of these tendencies or sequential schemes is that what counts as possible or accessible is partially fixed ("biased") by what exists. Also, particular biases play a major part in what distinguishes a taxon as such. For example, the constraints said to be operative in production of the tetrapod limb are part of the set of causes which fix the range of structures and capacities that make tetrapods possible.

A related point made by MS et al. is "there is usually no reason to suppose that the developmental mechanisms in question arose because of the particular phenotypes that they make readily accessible." (1985, 269) Here we again see the positing of a distinction between the production and development of form and its utility or adaptive value. This distinction is consistent with much of Gould and Lewontin's anti-adaptationist process structuralist approach already discussed. As we shall see in my Chapter Four, Amundson (1994) further articulates this view as the distinction between constraints on form and constrains on adaptation, though Dennett will disagree. The controversial consequence of this is that the production of variant phenotypes is accidental or random relative to the demands of adaptive evolution. (Maynard Smith et al. 1985, 269)

According to the above taxonomy of constraints, phenotypes that are inaccessible given *any* developmental mechanism seem to fall under MS#1 and MS#2. Also included under these categories are physico-chemical processes that occur independent of biological beings and thus are explainable without reference to natural selection. Two more examples of this are banding patterns on gastropod shells that result from standing or travelling waves of pigment formation in the mantle and geometrically similar pigment

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patterns that occur on both feathers and the coats of mammals. (Maynard Smith et al. 1985, 269) What is argued by Maynard Smith et al. is that these physico-chemical processes are "easily generated" even though the circumstances in which they arise or are deployed are quite different (gastropod shells, bird feathers, etc.) This kind of phenomena is recognized by many major commentators but there is no terminological consistency in regard to their identification and categorization and in many cases the categories that are offered are not entirely co-extensive. For example, the gastropod phenomena just cited could be classifiable as "architectural constraints" for Gould and Lewontin (CH2, III.2), "good tricks" for Dennett (1995, 77-8, 130-1), "order for free" for Kauffman (Brockman 1996, 334-8; Kauffman 1993, xvii) and "generic forms" for Goodwin (1994, 98-106) They might also be included under a processual interpretation of the evo-devo category, "standard part." [Raff 1996, 326, 330, 428]

As process structuralists such as Goodwin (1994) and Newman and Muller (2000) argued, such physico-chemical processes are important causal factors in the understanding of biological form and its production because of their primary role in morphogenesis and the fact that they are causally distinct from, if not always opposed to, the action of selection. But, do these sorts of processes explain body plan production, or persistence, as Gould and Lewontin suggest, or are they merely part of the incredible variety of processes which selection distinctively employs? Again, Dennett favored the latter in his view of selection as an algorithm and developmental and physico-chemical processes as the "substrate." (Chapter Two, V.2) For their part, Maynard Smith et al. detach the notion of developmental constraints from that of body plans and, to a lesser extent, macroevolutionary patterns, thereby demonstrating two key ways in which they differ with the approaches of process structuralists. In the end, Maynard Smith et al.'s primary focus is on the relationship between selection and MS#4 while MS#1&2 are not considered to be of much evolutionary significance, contra Gould and Lewontin (1979). Such constraints are of evolutionary significance for the latter because they are major features in *Bauplane*. Gould's (1989a) is a case study in this regard (see CH2, VIII.2; CH5, III.)

IV. Neo-Darwinians in Developmentalist Dress: MS et al.'s Obscurantist Selectionism

Despite their "developmentalism," Maynard Smith make no strong case for the evolutionary significance and/or prevalence of developmental constraints. Although, Resnik (1995) argues that they never even challenge neo-Darwinism, I do find their consideration of developmental processes to be in depth and varied. (See Ch. 5) But their neo-Darwinian selectionism is especially prominent later in the essay when they become skeptical of both the frequency and the significance of non-selective, or "independent," DC's. One reason for their skepticism is that many of what process structuralists would label as DC's are, according to MS et al., actually caused by a mode of selection not always invoked, and in other cases, selection is a co-producer of the constraint. Broadly, their line of reasoning is as follows: "Most populations, most of the time, are committed to particular ways of life." (Maynard Smith et al. 1985, 270) For example, changes that make kangaroos better at their current mode of locomotion (leaping) will be *selectively* favored over those that might eventually lead to a significant adaptive improvement (e.g. bipedal running) but initially are maladaptive. Thus, "one effect of selection is to limit the morphological and behavioral variations adequate to the tasks of living. By interacting with the developmental system, *such effects of selection bias the variants available* for subsequent selection to act upon [my emphasis]." (270) Here, the biasing is done by what is called "stabilizing" selection, not development.

The power of this view is aptly illustrated in the representations of adaptive landscapes. From such a perspective, a well-adapted mode of life is generally represented as either a peak or a point on a slightly uneven plateau thereby signifying a high fitness level in comparison with the other lower values represented by the "valley" below. In such a scenario, there are a few minor modifications that can be made which may alter the mode so as to increase its adaptive value, but switching modes (peaks or plateaus) requires a descent and another climb which obviously decreases adaptive value and requires an entire series of changes merely to restore the adaptive value obtained by the previous mode.(Kauffman 1993, 29-120) (This scenario, like the kangaroo case, assumes these modes are separated by "deep valleys.") Thus, for kangaroos, other ways of life or modes of locomotion are not inaccessible because of developmental mechanisms, rather, they are difficult to access because of the "conditions of existence" and the requirements of selection.

The above story seems an odd way of making a routine point: selection cannot demand short-term sacrifice for long-term gain since this would imply foreknowledge or some form of teleology. Yet, not only is selection not omniscient, it also lacks omnipotence. The constraints laid out by stabilizing selection for the preservation of some "way of life" are "local": that is, not only are they breakable, they get broken and some of these outlaws survive. An example is the tree kangaroo which climbs rather than leaps. (Maynard Smith et al. 1985, 270) Thus, just as many (local) developmental constraints are successfully breakable, so are some selective pressures.

It is often assumed, and sometimes demonstrated, that selection is able to override developmental constraints. (See my discussion of Dennett in the previous chapter). However, selection too is "overridden." The widely acknowledged phenomena of "genetic drift" offers a widely acknowledged set of cases. (Futuyma 1998, 297-300) As Gould and Lewontin put it, "alleles can become fixed in a population *in spite of natural selection*" due to random fixation or genetic drift. (Gould and Lewontin 1979, 82) Process structuralists claim that some morphological features caused by developmental constraints also occur in spite of selective pressures. They also claim that evolutionary *change* may be driven by non-selective factors. This view was addressed in my Intro in regard to Newman and Muller (2000) and will be further discussed in Chapter Six in regard to Gould's (2002) notion of "cross-level spandrels." With all this, the line of demarcation between "developmentalist" adaptationism and process structuralism becomes ever clearer: the former acknowledge that selection is restricted in ways traditional adaptationism failed to consider. However, process structuralists go much further since they argue that non-selective forces such as those found in to be operative in ontogeny play evolutionary roles not just as constraints but as creative and productive forces--i.e. they too are "evolutionary agents." Though Maynard Smith et al. lay the groundwork for such a view, their conclusion backs off from it (i.e. that stabilizing selection is the major player. (More below). However, co-author Alberch is one of the forerunners of this strong developmentalist view

IV.1 Alberch and the Problem of Form: Further Developing an Evolutionary Morphology

> Nature is not chaos, nor is it a boundless continuum of forms." (Alberch 1982b, 315)

The work of Alberch is of critical importance for the debates of this chapter and my dissertation as a whole because of the questions he poses and the way in which he further develops Gould and Lewontin's "structuralist approach" into a comprehensive theory of morphospace and developmental processes. Though he is one of the long list of authors of Maynard Smith et al. (1985), Alberch's view strongly diverges with the selectionist conclusions of that collectively authored essay.[69] Alberch's view is from the perspective of what he calls "evolutionary morphology" and focuses on the close relationship between morphology and ontogeny. This focus leads to the challenging of the adaptationist program and its tendency to atomize the organism into discrete traits and the corresponding failure to give due weight to the integration of the phenotype and organism as a whole. And, in a series of essays and experimental works (Alberch 1980, 1982a, 1982b), Alberch goes beyond the merely polemical. Though his work is influenced by and resonates with Gould and Lewontin's structuralist approach,[70] the

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[69] It is more efficacious to lay out Alberch's view first since it extends the discussion of the previous section. Also, there is some overlap between Alberch and Maynard Smith et al.—as is to be expected insofar as he is one of the authors! I will note these places of agreement as we proceed.

[70] He cites Gould and Lewontin (1979) and Gould (1977). Also, like Gould and Lewontin (1979), Alberch criticizes the adaptationist program for atomizing the organism into parts, and for not being testable.

questions he poses differ from and are more developed than "The Spandrels of San Marco [...]." This is largely why his work is invoked here.

Alberch is part of that long tradition--which began as quickly as Darwinism arose--of those who have questioned that random mutation/variation coupled with deterministic selection can explain morphological evolution. Like Francois Jacob (1977), he argues that contingent selective processes are too "sloppy" and cannot account for the ordered patterns that characterize both morphology and evolutionary change. Because of this and the related fact that the relationship between genotypic and phenotypic change is "nonlinear," Alberch shifts the focus from external selective pressures to the internal ontogenetic since this is the location of the constrained generation of variation that leads to directionality in macroevolution. (1980, 564; also 1982a, 29)[71]

Alberch's view has two interlocked dimensions. The first involves his theory of morphospace, the second his internalist and organocentric understanding of developmental processes. His view can be broken down as follows:

Alberch's Postulates

1) phenotypic variation is definitively bounded (Maynard Smith et al. 1980, 271); (a classic process structuralist postulate)
2) the generation and distribution of forms is generally independent of adaptive value (Alberch 1982a, 23);
3) the areas of biology best suited to study the generation and distribution of morphologies are those areas that have been displaced by the adaptationist

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[71] His opening example in "Ontogenesis and Morphological Variation" is the transition from cynodont to mammal. (1980, 653)

paradigm: embryology/developmental biology, paleontology, and morphology. (1982a, 30) Those in evo-devo strongly endorse this last claim (see Raff 1996, 424-7) Of particular importance is the study of development and those "complex systems" active in the generation and reproduction of organic form.

4) Developmental mechanisms possess a stability unto themselves; that is, they are integrated sets of stable processes and states that, in general, have the capacity to resist much perturbation, whether environmental or genetic.
5) In sum, and as such, evolution is to be defined as the "differential survival of morphological novelties." (1980, 653)

IV.2 Boundedness and Variation in Morphospace

> Alberch's concept of constraint doesn't deny selection, but rather, indicates that what is selected for and how the system responds to selection do not necessarily map onto each other very closely. (Raff 1996, 299)

There is broad agreement that extant adult phenotypes lie within a significantly limited range of "phenotypic space" or morphospace (the space of all physically possible and adaptively desirable forms). (Raff 1996, 30-9) Evidence suggests that the forms that do exist, and many of those that have existed, occupy only a very small portion of the morphospace, and these "occupied spaces" are definitively bounded. That is, there are groups of morphologies that form clusters and are "morphological neighbors," while other groups are separated by great gaps or stretches of empty morphospace with no intermediaries. Why? Some argue (e.g. Dennett, and many adaptationists) that enough time has not gone by for the vast reaches of emptiness to be filled. Indeed, they claim, maybe enough time will never go by since all life could become extinct first. Others argue that selective conditions have not warranted such a production of form. Alberch is dissatisfied with each of these replies.

The adaptationist view on distributions in morphospace is that phyletic trends observed in the fossil record--and patterns of change and diversity witnessed among living species--are to be explained in terms of their adaptive value and/or the competitive abilities that define the fitnesses of the new forms. Thus, the "establishment of a correlation between changes in the biotic and physical environments and change in the morphological structure is usually considered sufficient explanation in most evolutionary studies. The causal mechanisms are assumed" to be in agreement with neo-Darwinism[72], where "evolution is viewed as the interplay between effectively random genetic mutations with small phenotypic effects and deterministic natural selection." (Alberch 1982b, 313-4) The assumption is that selection operates upon a random and boundless supply of variation limited only by the conditions of existence, contingency, amount of time, etc. (Alberch 1982, 313-4)[73] Alberch disagrees:

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[72] For Alberch, "neo-Darwinism" is that version of the Adaptationist Program as outlined by Gould and Lewontin that argues that the gene is *the* unit of selection. This is not a necessary feature of the AP; group and organismic selection are permitted if not frequently espoused.

[73] It needs to be noted here that figures like Kauffman, and Dennett, recognize genomic constraints (as I've argued already) and thus Alberch's characterization of the AP doesn't apply to the more sophisticated reverse engineering perspective of Dennett. However, it is my contention that Alberch's developmentalist approach offers much, though there are problems and restrictions as I note at the end of the chapter.

> If a continuous distribution of genotypes can result in a discontinuous distribution of phenotypes then the discontinuities must be a product of the nonlinearities and thresholds in the mapping function between genes and phenotypes. [...] What controls the boundaries and thresholds and how resistant to selection are they? (Alberch 1982, 319)

Alberch's point here is about the relationship between genotypic and phenotypic change. According to the classic Darwinian model, evolutionary change in any lineage is small and gradual. This is true because the production of genetic variance proceeds via small, incremental steps as mutations occur rarely in each generation and only at small numbers of loci. Alberch's view does not deny that there are other sources of genetic variance—e.g. chromosomal mutation and transposition, recombination, etc. (Futuyma 1998, 267) His point is that when small and continuous genetic variation does occur, discontinuous morphological transformations will sometimes arise. There are many reasons for this: sometimes genetic change has an additive effect. That is, as mutations pile up, a morphological shift occurs. Othertimes, genetic change on one feature may change a cellular environment which indirectly effects other morphological features. For example, changes in the direction in which cells fold is oftentimes due to the mechanical properties of cells. These cellular properties may or may not be effected by particular genetic change. Bird feathers and mammalian hairs are a good example of such a morphological discontinuity.

Invagination is a process where a layer of cells (epithelium) is "tucked-in" so that a pocket is formed and the pocket opens onto the original surface. Evagination also

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involves the folding of a sheet of cells but instead of being tucked-in. the sheet of cells is turned inside-out. (Roughly speaking, a pants pocket is structurally akin to an invagination. Evagination occurs when one empties them by pulling out the pockets so that they protrude from the pants and are exposed inside-out.) Mammalian hair follicles are formed through invagination, and bird feathers (papillae), like reptilian scales, are formed from evaginations. What determines whether the epithelium buckles inward (follicle) or outward (papilla) depends on the contractile properties of intracellular filaments. (Futuyma 1998, 662-3) Thus, the difference between the occurrence of evagination rather than invagination is due to a structural-mechanical property of the cells. There are three key points here: 1) the two morphologies are discontinuous--there is no intermediary state of half invaginated and half evaginated. 2) The production of the difference is due to a threshold effect having to do with the mechanical environment of the sheet of cells as it relates to its substratum which is a relatively inelastic base membrane. (Futuyma 1998, 663) Therefore, the two morphologies are discontinuous even in cases when caused by continuous genetic change (e.g. an incremental change at a single locus). 3) It is also possible that the cause of the morphological discontinuity is not even genetic since factors such as calcium concentration may have altered the intracellular environment and led to the change. (Goodwin 1994, 167)

Furthermore, for Futuyma, Goodwin, and Alberch, and process structuralists in general, e/in-vagination is a developmental mechanism that is also a complex system (MS#2). Such systems, as Alberch argued, "often have nonlinear properties, so that a small change in one variable component can, by crossing a threshold lead to discontinuous differences in other components." (Futuyma 1998, 663) In this case, an incremental increase in the contractile strength of the intracellular filaments can lead to a change in the direction of the buckling. Furthermore, this developmental mechanism is a common one. It occurs in gastrulation (a subphylum-wide process) and in taxa specific morphogenesis. For example, cell foldings and discontinuous "pockets" occur in rodents. Geomyoid rodents such as pocket gophers and kangaroo rats have fur-lined external cheek pouches, while other members of the taxa have internal pouches (the ancestral condition.) (Robert 2002, 18-9) Robert ruminates,

> That such a small change in a developmental mechanism can have such a dramatic effect, coupled with the fact that no living geomyoids have both internal and external pouches, suggests there is no intermediate ancestor between rodents with internal and rodents with external pouches. (It would be difficult, both developmentally and functionally, to have both internal and external pouches.) (Roberts 2002, 19)

As such, the above episodes illustrate how morphological shifts such as from scale to follicle are dependent not just upon the external (selective) pressures, but the internal dynamics of the relevant ontogenetic mechanisms (e.g. cell sheet buckling). Adaptationism cannot explain the generation of these distinct morphologies nor can it always explain why the switch occurs. For Alberch, at its best, the AP can predict what trait is more likely to spread through a population once it has appeared—this is after all, what the notion of fitness entails. But, it cannot address the question of what was or is more or less likely to be generated. (Alberch 1982b, 314) For this, the focus must go even deeper into the epigenetic-developmental.

IV.3 A General Theory of Development

Developmental processes are complex, nonlinear, dynamical systems "characterized by a hierarchical organization that can be divided up into three interacting levels." (Alberch 1982b, 328) First is the genome itself and its relationship to protein assembly. Second are the cooperative, co-producing relations among enzymes and proteins which interact and "self-assemble" according to various physico- and biochemical "laws." Examples of these include the cellular properties relevant to morphogenesis: cell adhesion, motility, and contractile properties. All of these properties are directly determined by their constituent molecular parts. This second epigenetic level also includes proteins mediating cellular inductive abilities. For example, surface proteins can act as hormone receptors. Also,

> cells produce proteins that can diffuse and interact with the products of other cells and their surrounding embryonic environment. These patterns of biochemical activity can influence morphogenesis by providing positional information to be interpreted by the cells for differentiation purposes. Diffusion-reaction models belong to this class of phenomena. (Alberch 1982b, 320; also note MS et al. co-author Goodwin (1994, 42-59)

The third level is composed of the tissues that interact in complex ways according to sets of the well-defined rules of developmental biology--such as the ectodermal-mesodermal interactions in limb development, a favorite case study for morphologists. (Alberch 1982b, 320) According to Alberch, levels 2 and 3 are under genetic "control" but cannot be reduced to that level. (Alberch 1982b, 321) If this is true, then from a genocentrist perspective, selection might be considered to be the prominent agent in guiding development and the production of phenotypes. Alberch argues against this, but he may unwittingly open a window to the genocentric AP/RE on this point.

According to Alberch's schematic, "evolution can be viewed as the process of phenotypic transformations resulting from genetically mediated perturbations of these basic developmental parameters through phylogeny." (1982b, 322) The dynamics of developmental mechanisms determine their properties and their effects in and on evolution. Genes are a part of this dynamic, especially as parameters and mediators, but the *dynamic* cannot be understood in terms of the genes. He writes,

> The complexity of interactions during development renders the analysis of the parameters of morphological evolution impossible to reduce to a problem of changes in gene frequencies. Indeed, there is generally little correlation between rates of structural gene evolution and rates of morphological evolution. (Alberch 1982b, 664)

During development these *epigenetic* interactions constrain morphological change in evolution. Such mechanisms "define the apportionment of phenotypic variation upon which selection operates." (Alberch 1982b, 313) This results in discontinuities among morphological neighborhoods and directionality in transformation over macroevolutionary time. As such, extensive consideration of developmental mechanisms as a distinct level of phenomena is essential for understanding phyletic trends in evolution "since developmental interactions basically define the universe of possible morphologies and impose limits on the directional action of natural selection." (Alberch 1982b, 313) Some of these limitations are due to universal and complex systems constraints (MS#1 or #2) since "some morphological variation is not produced regardless of how adaptive it is" (Alberch 1982b, 326). Others are local: some traits that are fixed in some species are variable in others (DC's MS#4), still others exhibit a tendency towards the appearance of atavistic forms. (Maynard Smith et al. 1985, 271) The consequence of these last examples is that morphological variation is "nonuniform." Again, certain variants are much more accessible than others. (Maynard Smith et al. 1985, 271-2)

IV.3 On the Stability of Developmental Mechanisms and the Hierarchical Nature of Ontogeny

Epigenesis, as Alberch uses the term, implicates an anti-adaptationist, anti-genocentric, developmentalist and organocentric approach to ontogeny. What Alberch is most interested in is not gene sequences and frequencies but developmental mechanisms themselves. As noted above, such mechanisms include combinations of gene products, physico-chemical processes (e.g. calcification, adhesion) and cellular activities (invagination, mitosis) that are configured so as to become the processes of morphogenesis (from gastrulation to shell formation and organogenesis). This understanding is congruent with the contemporary view on the fundamental problem of morphogenesis: how do specific ontogenetic and adult structures arise and what leads to their positioning in both development and function? (Gilbert 1997, 701) For example, in the case of the limb bud, not only are cellular differentiation and adhesion of interest, but so is the formation of the limb bud, the induction of the apical-ectodermal ridge, the generation of the proximal-distal axis, the role and timing of Hox gene expression in its specification, and the further growth and patterns that cause the emergence of digits in a particular sequence and so forth. (Gilbert 1997, 701-27)

Alberch is not just interested in the details of these systems, but in the production and stability of the dynamic that emerges and furthers these interconnected processes. Here we see one element of what Gould and Lewontin referred to as the "tight integration of development": developmental mechanisms are resistant to much genetic and environmental perturbation during ontogeny. Alberch argues that this resilience is due to "epigenetic regulation." That is, both the environment and the genetic are sources of perturbations throughout development. The reason why phenotypes are not so easily derailed and can be modified only in certain ways is because like physiological systems, they are well-buffered and "homeostatic." (Alberch 1980, 654)

Homeostatic systems are able to exert control of over a set of variables so as to preserve system function. They do this by monitoring the values of these variables and restoring them when they depart from the permissible range. Such regulation and restoration is often accomplished via negative feedback processes. (Thain and Hickman 1994, 304-5) This understanding of ontogeny is also an intrinsic part of the view of MS et al. co-author Kauffman (Kauffman 1993 xiii-xviii, 173-234; Brockman 1996, 334-40) Again, as Alberch argued earlier, genetic mutations are not expressed randomly at the morphological level. Additionally, genetic variation is distributed continuously, but morphological variation at the macroscopic level is not. The latter is distributed among a finite set of discrete states. (Alberch 1980, 654)

For Alberch, there are two kinds of phenotypic variation: the discrete distribution of "steady (morphological) states" and the continuous variation that happens within these bounded domains (the "steady states"). (1980, 655) Although the mutations occurring at the genetic level are random, the transition from one steady state to another is not. (656) What becomes of interest, then, are the thresholds which demarcate the discontinuous regions of variation. Alberch, like Maynard Smith et al. (1985), argues that *developmental* canalization, stabilizing selection, and developmental homeostasis are the key factors. (More below.) The evidence for all this is that a wide variety of morphologies are never produced (Alberch 1980, 655), some appear much more frequently than others (659), and only some novelties recur (664). Also, cases of homoeotic mutants illustrate the nonrandomness and directionality of change and the phenotypic consequences of most, if not all, homoeotic mutations are mimicked by environmentally induced changes of the phenotype (they are "phenocopies"). This shows that in some cases it is the perturbation of the developmental mechanism as such that is at issue, and not just genetic variation in itself. (See also Alberch 1980, 658, 660) This point is also demonstrated in the cases where different genetic variations lead to the same phenotypic deviation, such as in winglessness in chickens. (663)[74] All of this is in

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[74] For more on all these points (stasis, perturbations, boundary domains), also see Alberch (1982b, 322-6).

explicit contrast to the AP which, for Alberch and Gould and Lewontin and many others suffers from a methodological flaw because its focus on the "microscopic" changes due to selection make the limits on selection hard to recognize. (1980, 655) Put another way, the exclusive focus on selection and "small, continuous, and gradual (genetic) modification" fails to glimpse the big macroevolutionary picture and the role of developmental mechanisms in the ontogenetic production of those phylogenetic patterns of change and stasis.

In addition, according to Alberch, speciation itself is a discontinuous, nonlinear transition between morphological steady states (species). (Alberch 1980, 664)[75] Such morphological evolution is the product of *regulatory* changes during development, as in heterochronic perturbation (660-2) and the alteration of the timing of cell differentiation and termination, the rate of cell proliferation, the rate of change in shape, and initial size. Sometimes, Alberch claims most of these are controlled by the interactions of several genes, but at other points he does not consider these productions to be under explicit genetic control. In any case, Alberch argues that evolution results from shifts in the distribution of these "developmental controlling parameter values," especially in regard to the timing of differentiation. (1980, 663) Again, sometimes, these parameters may be genes, sometimes they may not be. But perhaps even more crucial is that the *distribution* of these values is not under genetic control. (Ch 6, II.2 and VI.2)

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[75] Note that for complexity theory-inclined structuralists espousing the *Bauplan* Paradigm, the steady states of major interest would be the *Bauplane*, that is, groups of species. Thus, much speciation would be characterized as happening within some taxon (steady state).

While it is my view that Maynard Smith et al. (1985) are quite cautious, and in the end, downright skeptical, about the possibility of constructing a general theory of development and the evolution of form, Alberch is more optimistic. Alberch is interested in morphological trends in evolution and not just restrictions and constraints in themselves. That is, it's not just a matter of looking at what regions of morphospace are occupied, but determining the temporal order of the occupation. These trends, he argues, are controlled by the interaction among

> 1) the developmental dynamics (which control the recurrence of morphological novelties),
> 2) stabilizing selection (which aims to prevent any decrease in fitness), and
> 3) ecological parameters such as population size and breeding structure (which, acting in concert, determine the probability that new morphologies will become fixed). (Alberch 1980, 664)

This understanding of trends echoes Van Valen's proclamation that evolution is the control of development by ecology, though Alberch obviously focuses much more on the "development" side of the equation. Alberch also sees his view as being compatible with the punctuated equilibrium theory of evolutionary change and stasis. (1980, 664) A key implication of this view is that phylogeny is best understood more in terms of Waddington's (developmentalist) epigenetic landscapes and Thom's (structuralist) morphological formalizations rather than the AP's adaptive landscapes. (1982b, 324)

Here Alberch seems quite in line with the Gould (1971) of "D'Arcy Thompson and the Science of Form." However, in regard to Van Valen's definition of evolution, Alberch seems a bit more internalist if not orthogenetic, perhaps problematically so. There is little specific consideration of ecology in Alberch's work, unlike in Gilbert (1997), for example, and as Weele (1999) argues for more of.

V.1 Conclusion on Alberch and Key Elements in My Own View[76]

In sum, for Alberch, only some regions of morphospace are occupied and there are a limited number of evolutionary pathways by which these regions come to be occupied. (1982b, 314) This is due to the dynamics of development which includes both genome organization, epigenetic interaction, developmental mechanisms, and the processes of morphogenesis. (1982a, 19) What this means is that there are internal constraints on morphological transformation and these constraints are largely due to the field dynamics and stability requirements of developmental mechanisms.

The role of the developmental mechanism is twofold. First, it is generative. Thus, its structure, and not selective pressures, defines the realm of possible novelties. Second, it is regulative: the interactions occurring during ontogeny are homeostatic; they can accommodate and/or act as buffers to genetic and environmental perturbations so as to result in the production of an integrated phenotype. (1982a) Although the developmentalist AP does acknowledge that genes are both dependent upon and active within this developmental dynamic, in the end it disputes or ignores both of Alberch's claims. The AP understands evolutionary change in terms of selection and fitness and

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[76] Throughout this section I shall highlight those points by Alberch which I draw upon to build my own view, especially as laid out in Chapters Five and Six.

denies the integrity of the organism by atomizing it into discrete traits. Alberch argues that morphological kinds are discrete, hence the "morphological neighborhoods" with big gaps between them. Also, as in Gould and Lewontin (1979), what the AP often considers to be a "trait" is oftentimes not subject to selection.

For Alberch, then, evolution is the product of two relatively independent processes. The first is the *generation* of new morphological organizations or *Bauplane* (1982a, 22-). The second process is constituted by the interactions between the organism and the environment resulting in the *adaptation* (or annihilation) of the organism. Mechanisms controlling development and adaptation are independent (1982a, 23). This is consistent with Gould and Lewontin's distinction between those forms resulting from architectural and developmental constraints that are "deeply integrated," and those traits which are due to selection. Put another way, the processes involved in the production of *Bauplane* are separable from those responsible for the modification of various elements comprising the organism. But, for Alberch, in contrast to Gould and Lewontin, architectural constraints are developmental. As I argued in Chapter two, Gould and Lewontin made a mistake here, and my own view is with Alberch.

Like Gould (1977), Alberch believes that changes in developmental timing are a major factor in the creation of morphological change and the content of these alterations are due less to selection and environmental change than to the internal structure of development. What follows is that the unrivalled primacy of adaptation in understanding evolutionary change and stasis is challenged. Natural selection, for the most part, eliminates excessively unfit forms and modifies the others, but it generates none.

Another implication of this view, Alberch claims, is that this developmental approach explains what population genetics cannot: the production of novel traits. (1982b, 328-30)

V.2 On the Production of Novel Traits

In a dramatic reversal of the common notion that developmental constraints restrict the action of selection, Alberch argues that DC's may open up new adaptive realms. (1982b, 329-30) MS et al. co-author Kauffman would seem to agree (Brockman 1996, 335-6) The effects of some sets of perturbations pile up so as to actually push the system across a threshold, but others do not precisely because of the morphological nonspecificity of mutations and the discontinuous nature of the genetic changes discussed above.[77] This allows transformations to occur that override the functional constraints that greatly limit the gradualist action of directional selection (as in the previous case of the kangaroo). (More on this in Chapters Five and Six.) This kind of change pushes the phenotype into a new stable state and, subsequently, a new adaptive ball park. (Alberch 1982a, 25). This is perhaps Alberch's greatest contribution to the developmentalist and/or process structuralist program(s): ontogeny itself, independent of selective pressures, is a creative force in the evolution of morphology and needs to be studied as such. A consequence of this is that many evolutionary novelties cannot be explained by selection. Building upon Alberch's view, I will argue in Chapter Six with Gould (2002) and Newman and Muller (2000), that process structuralism indeed has much to offer for understanding the production of morphological novelty.

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[77] Quantitative changes in the basic parameters of development may result in qualitative changes in morphology; that is, rather than an altered old feature, the emergence of a new one. The parameters, as we have seen, are growth rate, inductive ability, cell adhesion, and most other cellular physico-chemical properties.

Another consequence of this approach is that equilibrium models of evolutionary change (Alberch 1980, 664) may be developed such that "if a macroscopic methodology is constructed, like continuum or statistical mechanics, we can then make predictions and study the behavior of these media." (665) Alberch, unlike Dennett or Mayr for example (Mayr 1982, 37; 57-9), is keen on the idea that evolutionary theory should be able to make predictions about evolutionary change (i.e. morphological impossibilities and probabilities). The process structuralist project, then, would significantly increase the explanatory power of evolutionary theory. Again, Alberch is a process structuralist because he endorses both main tenets: 1) the space of all possible phenotypes (design space) is highly constrained, and 2) many of the organizational features of organisms are explained by intrinsic physical constraints such as those resulting from developmental processes. Here he extends the second point to argue that the various mechanisms operative in ontogeny are, at times, creative from an evolutionary perspective.

VI.1 Maynard Smith et al.'s Selectionist Developmentalism

With Alberch's position now laid out, it is easier to follow the moves that are made in Maynard Smith et al.'s (1985) concluding sections. What happens is that although Alberch's view seems to build upon, and/or influence MS et al.'s taxonomy of constraints (MS#1-4), his process structuralist account is displaced along with the project to explain patterns of morphological stasis and change in evolution.

MS et al. argue that two agents are responsible for the production of morphological change and stasis: selection and development. This leaves us with three possible scenarios:

1) selection guides development (strong version of this view is the optimizing AP: selection rules over and overrides all)
2) development biases variation which then decreases the range available for selection (strong version is internalist neo-"orthogenesis": development determines the possible macroevolutionary pathways)
3) development and selection often act in tandem as inextricably linked co-producers of constraints

Although it is possible, or even likely, that all three of these are operative at different times and on different traits, lineages and so on, can the three be ranked in terms of either significance and/or frequency?[78] As we have seen, many adaptationists would favor the first: development is subordinate to selection (genes set the parameters if not govern the processes). Alberch argues for a strong version of the second: selection modifies individual forms and *Bauplane*, but the production of these forms is not only independent of selection, it is the precondition for selection. A version of this view was also put forward by Gould and Lewontin (1979) and Kauffman (Brockman 1996, 335-6) when each discussed the conditions that must be met in order for adaptation to be possible. Gould, especially in *Wonderful Life* (1989), seems to favor a historicist version of the third. Such a view would place historical-ecological contingency at the center rather than development or selection. Maynard Smith et al. (1985) confess uncertainty and claim

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[78] The difference between frequency and importance may fit within Alberch's distinction mentioned in the section above where mutations pile up and a threshold is crossed. On other *Bauplan* inclined views, selective change is more frequent but minor because it is developmental changes which bring about major changes in body plan.

that, in many cases, it is difficult to determine whether development OR selection is the sole cause of a given trait. (Maynard Smith et al. 1985, 275) Yet, in the end, they strongly lean in the direction of option one: selection guides development. This shift comes to the fore in their discussion of canalization and "stabilizing selection." Early in their essay, this mode of selection emerges as the principal cause of DC's, but later it is deemed less important and frequent. Such shifts in position is one of the reasons that MS et al. is far too slippery to constitute the received view on constraints.

To understand the causal role of constraints and development, one must do more than just look at the range of biological forms matched against the space of possible forms (morphospace) and ask "why all the empty space?" An examination of existing populations and the way in which they develop, survive and reproduce is also required. As was noted above in the case of kangaroos, Maynard Smith et al. (1985) argue that "Most populations, most of the time, are [...] committed to particular ways of life." (270) What this means is that "one effect of selection is to limit the morphological and behavioral variations adequate to the task of living."[79] Thus, in populations which are successful and relatively stable in numbers over long periods of time, selection may act with or upon development in order to reduce the amount of variation, the variability of mutant phenotypes, and phenotypic plasticity. (270) Such reduction in the *production* of variation is called "canalization." Canalization is not to be confused with stabilizing selection. The latter, like all modes of selection, requires that there be heritable variation

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[79] One substantiated argument for this is that newer populations or races show more phenotypic variability than older ones. The authors cite the case of two races of *Drosophila* on Hawaii where the number of bristles on the tarsus used by the males in courtship is conspicuously more variable in the newly evolved role than in the adjacent older row of bristles. (Maynard Smith et al. 1985, 270)

since, by definition, there can be no selection without heritable variation. Canalization (Weele 1999, 27-31) in its narrowest and most helpful sense, refers to a developmental mechanism which is not producing much morphological variation—subsequently, there is no heritable variation. Unfortunately, the term "canalization," like its kissing cousin "generative entrenchment," (Wimsatt 2001) is not used consistently in the literature. The reason for this is that though both refer to the phenomena of ontogenetic resistance to change and/or the reduction of the production of phenotypic variation, there is no consensus on the cause of such entrenchment.

The trick lies in determining whether this bias, and indeed, limitation, upon the variants available for subsequent selection results from selection's earlier modification of the developmental process (Option 1 above) or the inherent, "internal" dynamics of the developmental mechanism itself (Option 2), or the interaction of the two (Option 3). As we have seen, Alberch separates the production of form from the process of adaptation, thereby isolating the forces of selection from the processes of development. As we shall see, Maynard Smith et al. argue that this rarely happens, thus evolutionary stasis and change must be explained with a different model. Such a model places selection at the forefront, though in a way it is often interlocked with developmental processes.

VI.2 Stasis and Change; Canalization and Stabilizing Selection

MS et al. argue that there are cases where ontogenetic refractoriness or narrowness is actually the result of "stabilizing" selection. As noted before, evolutionary stasis of some trait or form may be a result of the fact that any modification of this form would lead to a decrease in fitness. The most obvious case is one where the lineage reached an adaptive peak and its population and local environment remained stable over the next many generations. Departures from the peak occasionally occur but they are always eliminated.

However, evolution is infamous for not being characterizable in such simplistic ways. For example, a change in the local predator may lead to adaptive changes in one population but not another (Vermeij 1987, 373) Also, morphological change often does not occur when environmental conditions fluctuate rapidly and frequently. For example, ostracode lineages (a type of crustacean) of the Atlantic coastal plain of the US underwent little morphological change when climactic and oceanic conditions were constant, nor did they change when glacial and interglacial episodes followed each other in rapid succession during the Pleistocene. The morphological change that did occur was concentrated during "long-term changes in climate and oceanic circulation especially during the Middle Pleistocene (3.1 to 3.6 million years ago) when the Atlantic and Pacific Oceans became separated by the uplift of the Central American isthmus." (Vermeij 1987, 374) But, more critically, stability of environment does not guarantee lack of modification, especially in less mature species. (Maynard Smith 1985 et al., 270-1) And again, degree of "maturity" refers to the stability of the internal organization and its elements, not to morphology or the relation of morphology to selective pressures.

However, it does seem that once a species is adaptively established or "mature," it reaches a kind of optimum or equilibrium position (adaptive peak)[80] in regard to its niche, so long as the latter is stable. The consequence of this is that in such cases, adaptive, and presumably morphological, change nearly ceases. (Vermeij 1987, 374; Maynard Smith et

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[80] The notion of adaptive peak is frequently invoked nowadays, as opposed to in 1985 at the time of Maynard Smith et al. and the preceding decade of Alberch's work.

al. 1985, 270-1) Though Vermeij argues that certain changes are obviously too fast to adapt to (the dramatic decrease in biodiversity over the last century is certainly evidence of that), he does not favor a gradualist conception of evolution. Vermeij argues for the punctuated equilibrium view: that is, once established, a species tends to be adaptively static, and when change does occur, it is copious and rapid. (1987, 374; 371-6)

The evidence for this is diverse. Citing a line of work that goes back to Waddington (1957) and Haldane (1954), Maynard Smith et al. observe that "many natural populations are rather uniform morphologically, whereas populations carrying a mutant that disrupts significant features of that morphology are highly variable." (1985, 270) The authors cite additional evidence (Carson, Val, Simon, and Archie, 1982) that populations that have recently experienced an adaptive change remain much more variable than those populations that have been unchanging for longer periods of time. These questions of evolutionary stasis quickly lead one into controversial territories over whether evolutionary change is predominantly gradual or punctuated (and whether the fossil record could ever tell us).[81] (Vermeij 371-6) However, the common view is that species that have been stable over long periods tend to remain at or near that equilibria. (Futuyma 1998, 421-7) Especially, if there has been little local environmental change.

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[81] For a non-genocentric adaptationist perspective on adaptive change resulting from selection see Vermeij (1987, 371-6). For example, in the case of butterfly mimics, Vermeij favors Turner's model which understands adaptive change to consist of two phases: the first involves a series a rapid adaptive changes that prescribe further change; the second involves "a slower phase of gradual modification, which increases the effectiveness of the aptation." (Vermeij 1987, 372) (The term aptation is meant to indicate agnosticism as to whether selection and genetic change are at work in the case.) Vermeij's overall view on the matter seems to be that if the environment remains stable, "further adaptation usually ceases, and the population becomes adaptively static." (373) That is, the population is no longer able to undergo adaptive change. He does not specify whether this is due to development or stabilizing selection. (371-6)

(Vermeij 1987, 372-4) Also, selection tends not to favor pronounced and rapid change in any one character. (Futuyma 1998, 421)

The reason for the details in the last couple paragraphs is because the view that asserts that stabilizing selection, rather than DC's, explains patterns of morphological stasis and change undermines part of the attractiveness of process structuralism since the latter purports to explain what selectionist explanation cannot. As MS et al. claim,

> the operation of stabilizing selection on a character with heritable variation, or a fluctuating directional selection on that character in an appropriate succession of environments, suggests that *developmental constraints are not required to explain evolutionary stasis* [my emphasis]. (Maynard Smith et al. 1985, 276)[82]

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[82] A few points need to be made here. Maynard Smith et al. (1985) argue that selection may not only limit the variability of mutant phenotypes (270), it also eliminates heritable variation (e.g. produces a canalization). While in the above I argue as if MS et al. are right on this point, it is worth noting that more recent lab studies cited by Futuyma, however, disputes this, stating that while *phenotypic* variation is limited, genetic variance and heritability remain high. (Futuyma 1998, 421) If this were the case, MS et al. are still wrong and Alberch, and process structuralism are still right: genetic variance then does continue to arise but is absorbed by the developmental mechanism and the morphology remains relatively uniform. All this is important for our purposes since Maynard Smith et al. (1985) have offered a wide array of possibilities for constraints on form but as the essay progresses, the focus narrows and stabilizing selection and canalization rises to prominence over developmental constraints. (Maynard Smith et al. 1985, 272) Also of relevance is the power of directional selection which sometimes overlaps with stabilizing selection. (Futuyma 1998, 424) Also, conflicting selection pressures may lead to stabilizing selection, as in the intermediate bill size of finches on the Galapagos. (Futuyma 1998, 422-3) For Futuyma, stabilizing selection is connected with the trade-offs view which understands many populations to have evolved traits that are intermediate optima; compromises or balances struck as various characters each reach equilibria. (424)

As MS et al. tell it, stabilizing selection is a kind of *selective* constraint. This view argues that "some developmental constraints are themselves the result of selection and are not automatic consequences of the developmental system." (270) With this move, the adaptationist appropriation is now complete: yes, there are developmental constraints, and yes, they are sometimes significant, but if so they are products of selection. And note that Gould and Lewontin actually permitted this understanding of DC's since they were deemed to be *phyletic*, not architectural, constraints.)

Many, such as Dawkins and Dennett, would be quick to stress the importance of stabilizing selection since it, and not development as such, could be the cause of evolutionary stasis when there is no observed variation. However, Maynard Smith et al. argue that "once heritable variation is eliminated or becomes unavailable, features of the relevant phenotype are not maintained by selection, but are the product of a constraint." (1985, 277) *This is a critical point.* Again, stabilizing selection can only be said to operate when there is heritable variation existing or available. But what about those cases or traits for which there is no heritable variation available (if this indeed occurs, see previous footnote)? One reply is that, as they note in another section, certain genotypes are inaccessible given the present genetic system. That is, for phenotypic change to occur, there must be a series of mutations accessible to the lineage (a genetic pathway). (270) In this case, the past action of selection limit its future action, a classically phyletic constraint, or, in the classification scheme of MS et al., it is possibly a genomic systems constraints (MS#2), a DC!

Yet, even apart from the genomic constraints, there is an often overlooked problem with the conception of "stabilizing selection" and "canalization" (a DC caused by selection). In such cases, in order to understand the present morphology and future evolution, one must shift one's perspective from the action of current selective pressures to the structure of developmental mechanisms responsible for the invariant or pervasive trait. As I argued in Chapter Two, the production of this refractoriness or "phyletic inertia" marks a transfer of causal power from selection to development. This requires a subsequent switch in forms of explanation from the AP to a developmentalist approach. The same is true of the "canalization" of a developmental mechanism that is supposedly due to selection. Furthermore, even if this developmental persistence is "broken," it may still posses great evolutionary significance because it biased the lineage along one developmental and morphological pathway rather than another; that is, even though it did not shut off all other options, it pushed most variation in one direction. An already noted example of such biasing is "branching" in palms (III.1 above) (Additional cases will be discussed in Chapters Five and Six.) In sum, the invocation of Alberch combined with my criticisms of MS et al. adds up to a pluralist view where evolution is considered to be comprised of periods of production, change, and stasis where different agents--various modes of selection and developmental mechanisms, etc.--are active at different times, but selection cannot be said to be the sole guide.

VII. Conclusion: the Implications of the Debate: Macroevolution, Punctuated Equilibrium and Distributions in Morphospace

In this chapter, the many moves made by Maynard Smith et al. have been examined, additional research has been reviewed, and Alberch's conception of developmental mechanisms and morphospace has been articulated as an alternative. So where are we? Is the notion of developmental constraints crucial for understanding evolutionary stasis and change?

MS et al. argue that DC's are of evolutionary significance if they explain 1) macroevolutionary stasis; and/or 2) why certain regions of morphospace are empty and/or that others are tended towards (i.e. evolutionary patterns and trends). (281) Do they explain either?

VII.1 Explaining Stasis

Though the existence of morphological stasis in various lineages and phyla is not controversial, the explanation for it is. MS et al. (1985) argued that the "most interesting and paradoxical cases of evolutionary stasis" occur where there is considerable heritable variation. DC's, they argue, come into play only in the absence of heritable variation. Thus, the cause of such stasis must be stabilizing selection. So what about the cases where there is no heritable variation? First, they state, this is difficult to determine. Assuming that there is no heritable variation might a DC be the cause, as in the case of bilateral symmetry? Yes, but MS et al. (1985) point out that such cases are less numerous than previously supposed, precisely because stabilizing selection may be responsible for stases previously ascribed to DC's (where there was or is heritable variation). Second, the action of past selection may actually be causally responsible for (some) developmental constraints. That is, in many cases, but not all, DC's are phyletic--as Gould and Lewontin acknowledged. However, as was noted in my previous section, even if this is true, phyletic constraints require a developmentalist explanation.

VII.2 Explaining Evolutionary Trends and Patterns: MS et al. vs. Alberch and Process Structuralism

For Maynard Smith et al. (1985), there are many forces and agents operative in influencing morphological trends, or "pathways," in evolution. Development is among them. As such, the authors challenge the traditional AP view, first stated by Fisher and Haldane, that "directional bias in variation will not produce evolutionary change in the face of opposing selection." (Maynard Smith et al. 1985, 282) However, key among the challenges here are genetic system constraints--not only developmental ones--and the operation of cellular and chromosomal mechanisms that are affected by selection operating at these lower levels (281-2) They go on to argue,

> the fact that natural selection is such a multi-level process acting not only on these many lower levels but on "individuals, demes, species, and so on" means that whatever trends and patterns there are must be understood as extremely complex and subtle in their origins, and perhaps in their efficacy and power. Furthermore, there are many cases where it is difficult or even impossible to separate the contributions of developmental and selective factors in the etiology of a constraint. (Maynard Smith et al. 1985, 282)

Here we see a split with Alberch's hard and fast distinction between the processes of development and the processes of adapting organisms to their environments. Again, for Alberch, selection does not generate morphology, it modifies morphology. Contrarily, Maynard Smith et al. argue that selection modifies many levels of the developmental processes themselves. Such modifications are generative insofar as they shape elements of ontogenetic mechanisms. I will further examine the details of this debate in next three chapters, but for the moment I would point out that Alberch verges on an overly rigid developmental internalism if not outright orthogenesis. Not only does Alberch draw an uncrossable line between generative and adaptive processes, he argues that the generation of morphological organization proceeds independently from environmental factors. (1982a, 23) On this last point, I believe he goes too far. At other points, Alberch acknowledges that genes play a role in the establishment of developmental parameters and are "interactants" among other interactants in development (e.g. cellular and morphogenetic processes). (1982b) This is closer to my view. Yet, ultimately, the issue is not whether genes participate in development—they obviously do—but if selection's activity at this level guides developmental mechanisms and shapes macroevolutionary patterns. In my view, selection most likely does not since there can be no selection for long-term trends! It is my view that selection does occur at lower levels, e.g. genes and possibly developmental mechanisms themselves, but such selection is not of overwhelming evolutionary significance: that is, that such selection occurs does not mean that it produces most DC's much less controls development! Also, I agree with Alberch that the fact that organisms are homeostatic systems plays a key role in explaining the patterns of stasis and change and distributions in morphospace. This is especially true since homeostasis is a property which is central to the self-regulation of organisms and significant evolutionary change is due to regulatory changes in development (e.g. heterochrony).[83] This theory of organisms adds important detail and depth to Gould and Lewontin's "deep integration" thesis.

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[83] As I noted above, Gould regards heterochrony as quite significant and widespread,

VII.3 A New Taxonomy of Constraints

As we saw in Chapter Two, Gould and Lewontin's taxonomy of constraints broke down in regard to distinguishing architectural from developmental factors. Though they sought to maintain a distinction between the architectural and the developmental-phyletic, clearly the former sometimes if not always arises within development itself. MS et al.'s taxonomy rectifies this discrepancy by classifying "architectural constraints" as those arising either from physical and/or chemical laws and materials (MS#1) or from the dynamical demands associated with complex systems (MS#2). And, again, all four kinds of constraints are classified as "developmental."

But this reclassification precipitates an apparent paradox: although MS#1 and #2 may constrain developmental processes, each is nonbiological in origin. This is what, I believe, led Gould and Lewontin, following Riedl and Seilacher, to separate architectural and developmental factors. Ontogeny is obviously at least partially subject to all those contingencies characteristic of the evolution of life on Earth. If the tape were replayed, so the saying goes, evolution might have taken a very different course. This is one of the great themes of Gould (1989). Yet, development too is subject to the historically specific and shifting demands faced by living beings struggling to survive and reproduce. Unlike the most complicated of technological systems, each living must function as builds itself. And so long as there is function, there is competition, adaptation and selection.

But as I argued in Chapter Two, constraints that arise because of the employment of nonbiological phenomena cannot be due to selective pressures because they are

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Raff regards it as less widespread but still significant. (Raff 1996, 282-4, 427-8) constituents of the process, and any production process is highly dependent upon the properties of the materials available to it. This in no way denies the novelty of the processes of life and organisms in all their grand and dizzying diversity. Rather, it calls attention to life's continuity with the nonbiological and the manners in which materials and processes geological, chemical, and physical both comprise and are implicated in the development, structure, and function of all living beings. As such, on my view, physical-chemical (MS#1) and complex systems constraints (MS#2) are developmental because not only are they active in development, but there could be no ontogeny of living systems without them. However, they are not phyletic—i.e. that are not due to selective pressures.

The import of the above is that a limit is placed upon the applicability of the concept of stabilizing selection. MS et al. argue that, assuming heritable variation is available, constraints arising from the particular demands faced by developmental mechanisms are likely due to stabilizing selection. Yet, the key contribution of Alberch is that he calls attention to the *range* of heritable variation and argues that MS#1&#2 shape what is presented to various selective regimes, stabilizing or otherwise. (So do MS#4, but *some* of these may be due to past selective pressures.) What is especially absent in the conclusion of MS et al. is any consideration of the impact of constraints arising from physical-chemical factors (MS#1) and the dynamics of complex systems (MS#2) might have on the range of heritable variation that can be produced, macroevolutionary stasis, and, subsequently, morphological patterns and trends. Perplexingly, Dennett's reverse engineering approach did recognize such factors, but then he argued against their evolutionary significance. Alternatively, MS et al. repeatedly proclaim the significance of DC's, but then they take an adaptationist approach to their origin! Whereas Dennett claimed such constraints were able to be overridden by selection, MS et al. claim that such constraints arose because of selection—and may or may not be able to overridden by subsequent selective pressures. From my view, each omits a key piece to the puzzle.

VIII. A Final Summing Up: My View (First Take)

1. Process structuralists (including myself) claim that ontogenetic situations in which developmental processes are causally independent of the action of selection are both widespread and of evolutionary significance. As argued earlier (Intro, III.2; Ch1, II. and III.1), such causal independence may be argued for when there is no heritable variation in the population or the existence of the feature predates the selective pressure which it is currently employed. (Gould 2002, 1235) As laid out in the Intro (III.2) and Chapter Two, in many of these cases, the characteristics of the feature may be explained by the action of physico-chemical processes as noted by Newman and Muller (2000), Goodwin (1994), Gould and Lewontin, Seilacher, Riedl, Dennett and even Maynard Smith et al. or by traditional DC's of the "construction rule" sort. (More below.)

2. "once heritable variation is eliminated or becomes unavailable, features of the relevant phenotype are not maintained by selection, but are the product of a constraint" and must be explained as such (Maynard Smith et al. 1985, 277) DC's that arose because of selective pressures that eliminated heritable variation (i.e. they became a "canalized") are, and must be explained as, DC's since current selective pressures do not explain their persistence. This is true despite their original adaptive and/or selective origin.

3. The stability of environment (and the action of stabilizing selection) does not guarantee lack of modification, especially in less mature species. (Section IV.2 above) Also, degree of "maturity" refers to the stability of the internal organization and its elements, not to morphology or the relation of morphology to selective pressures. **In some cases, however, trait stasis is due to stabilizing selection and not DC's.**

A General Theory of Development

4.1 Organisms are homeostatic systems. The ways in which they change and do not change will be framed by this developmental-functional property/capacity. This is a more elaborated version of one aspect of Gould and Lewontin's "deep integration" thesis. Because of this, organisms persist despite much random genetic and environmental perturbation. Also, some evolutionary change involves changes in the regulation of developmental systems. Again, being homeostatic is more a capacity than a constraint since it enables modifications not endurable by non-homeostatic systems.

4.2 Ontogeny, and individual developmental mechanisms are both generative and regulative. This is consistent with organisms being homeostatic systems. The role of the developmental mechanism is twofold. First, it is generative. Thus, its structure, and not selective pressures, defines the realm of possible novelties. Second, it is regulative: the interactions occurring during ontogeny are homeostatic; they can accommodate and/or act as buffers to genetic and environmental perturbations so as to result in the production of an integrated phenotype. (1982a)

5. Population genetics cannot explain the production of novel traits (1982b, 328-30); only a process structuralist account is adequate. Alberch does not sufficiently establish this point, but drawing upon his view, I will argue in Chapter Six with Gould (2002) and Newman and Muller (2000), that process structuralism is better able to explain morphological novelty than population genetics and non-genocentric adaptationism.

6. A Pluralist, yet Developmentalist, Evolutionary Morphology: Both selective and developmental factors play significant roles in the production and evolution of form though at times they have crucially different roles (see above). The next task is to better understand the place and role of each. Chapter Four takes up the next step in this challenge and Chapters Five and Six lay out the details of and reasons for my pluralist account.

CHAPTER FOUR:

THE EFFECTS OF CONSTRAINTS AND INCOMPATIBLE FORMS OF EXPLANATION: AN IMPASSE WITHOUT A SYNTHESIS?

I.1 Summary

This chapter focuses not so much on the causal origins of constraints as on their effects. As was argued in Chapter Three, the approach of Maynard Smith et al. (1985) is unable to adequately assess the evolutionary significance of developmental constraints in the evolution of form. Apart from the array of problems discussed in the last chapter, there is an additional reason for the failure. According to Amundson (1994), two different strategies of explanation are employed during these debates. Adaptationists interested in developmental constraints seek to understand the ways in which developmental processes restrict the adaptedness of organisms. Developmental biologists interested in such constraints seek to understand how they restrict morphology. For Amundson, there are, then, two different research programs in operation, and the different forms of explanation employed are distinct and, in at least one sense, incompatible. Amundson finds this explanatory impasse untenable and concludes by calling for a "developmental synthesis" which would reconstruct the conceptual structure and research program of evolutionary biology by integrating a developmentalist and structuralist approach. Amundson's account of the explanatory impasse is largely convincing especially given connections to earlier work by Sober. Also, his cases studies—including several from Kingdom *Plantae*--and further articulation of the notion of morphospace aid our understanding of the methodologies of developmentalism and adaptationism. Amundson also remarks upon the importance of Alberch's process structuralism. However, his call for a "developmental synthesis" is underdeveloped such that little direction for such a synthesis is provided. In the next two chapters I will argue against such "Synthesis" talk. The chapter proceeds as follows: The Impasse Between Developmental and Adaptationist Explanations of Constraint, Amundson's Response to the Impasse, and Problems with Amundson's call for a "Developmental Synthesis."

I.2 Introduction

Amundson's work is useful for teasing apart the tangle in which Maynard Smith et al. entwine themselves in the concluding sections of their essay. As was discussed in Chapter Three, Maynard Smith et al. give at least three different reasons to doubt the claim made by structuralists such as Gould, Alberch and others that DC's are a significant factor in the evolution of organic form: the first is empirical: there actually isn't that much evidence of DC's especially when one notes that many constraints are due to canalization or stabilizing selection, not some developmental factor. The second is methodological: distinguishing between selective and developmental factors is extremely difficult, as is, supposedly, the distinction between genetic factors and other developmental factors or "interactants." However, MS et al.'s response is to treat these epistemological pains with a selectionist salve. This makes their approach/program, in the end, strongly adaptationist. That is, the recognition of the multidimensional interconnectedness among an organism's components parts and processes and the subsequent prescription for methodological caution weakens the case of those arguing that agents operating independent of selection exist or can be identified. This view is unduly obscurantist. Amundson offers a way of rectifying this while building upon the work of Alberch and introducing more cases.

Amundson (1994, 1998) argues that the problems posed by developmental constraints, complexity, and structuralist considerations—all acknowledged by Maynard Smith et. al. and Dennett—are not properly resolved by adaptationist views of *any* variety.[84] One of the ways that he does this is by drawing upon and slightly refiguring the work and approach of Alberch. As we shall see, this appropriation of Alberch is different that the one discussed in the second half of my Chapter Three. In sum, what Amundson thinks is missing from the whole debate over the nature and significance of DC's is an explicit distinction between DC's as a constraint on form and DC's as a constraint on adaptation. Developmental biologists and many process structuralists often focus more on the former than the latter, and adaptationists and neo-Darwinians focus almost exclusively upon the latter—with the exception of Dennett--whose work was published after Amundson.

I.3 Development, Adaptation, and Explanation

Amundson argues that a major misunderstanding plagues the debate over the nature and significance of developmental constraints in regard to the evolution of form. The misunderstanding concerns what relatively fixed or persistent developmental pattern can be said to constrain. As my previous three chapters hopefully have made clear, this

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[84] Amundson (1994) does not directly criticize Maynard Smith et al. (1985) The essay is, in fact, favorably mentioned (1995, 569), but this approving citation refers to an argument in the body of the essay, not its conclusion. (The agreement occurs because Maynard Smith et al. do not argue that developmental constraints reduce the adaptedness of organisms as Niklas does. Amundson also argues against the views of the latter. (1995, 567-70) See below.

misunderstanding is not simply a matter of terminological confusion or inconsistency. It is, rather, due to a difference in research traditions and their problems, concepts, methods and-- perhaps most critically for Amundson--the form of explanation constructed and the explananda sought.

Amundson initially identifies the differing research traditions as adaptationist "neo-Darwinism" that has developed since the Modern Synthesis and the opposing "general structuralism"[85] which he associates with embryology/developmental biology. (1994, 558) As argued in previous chapters, Amundson too claims that embryology was left out—and/or chose to opt out—from the Modern Synthesis and now developmentalists want to bring it back in to forge a "Development Synthesis," but not according to the terms of neo-Darwinism. (558)[86] The motivation for such a synthesis is due to the fact that neo-Darwinism's focus on natural selection has failed to appreciate the significance of developmental processes when explaining the production of organismic morphology and the patterns of change and stasis of such forms seen over (macro)evolutionary time. Although the debate over the existence and significance of developmental constraints is the primary stage where this conflict is waged, Amundson argues that much more than the significance of such "constraints" is at stake.

In mainstream adaptationist evolutionary biology, the most common view of DC's is not just that they are "biases," but they are restrictions on the adaptive optimality

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[85] Amundson's notion of "general structuralist" is consistent with my own concept of structuralism outlined in CH2, II.1.

[86] For a detailed historical account of this split from Amundson's perspective see his "Typology Reconsidered: Two Doctrines on the History of Evolutionary Biology." (1998)

of adult organisms. These restrictions are, rightly, considered to be due to the mechanisms active in the development of some class of organisms. Thus, "natural selection simply cannot overcome the conservative forces of development, and suboptimally adapted traits and organism are the result." (Amundson 1994, 559) We have encountered and examined this view throughout this dissertation (especially in CH's 1 and 2) and Amundson's explication of it is not significantly different from previously addressed formulations.

What is unique, however, is Amundson's characterization of the developmentalist structuralist program. Amundson argues that the major conflict between the two sides is over what is being explained: "Phylogenetically evolved adaptations are the primary explananda of natural selection, the central mechanism of neo-Darwinian theory" (Amundson 1994, 560), but they are not the primary explananda of developmental biology. (560-1) Developmentalists seek to explain form (563-4). Thus, "The constraint/adaptation dispute is unlikely to find quick resolution due to a deep contrast in explanatory strategies between the adversaries." (558) Just like debates over mutation in the early 20th century, this isn't just a semantic problem (cites Mayr 1980, 20ff): "The dispute, at bottom, is a clash of explanatory strategies, of approaches to explaining the nature of organic life." (559) Whereas Maynard Smith et al. focused upon evidence, method, and research strategies, Alberch's interest in explanation recalls Gould and Lewontin structuralist approach's and *Bauplan* Paradigm. (1979, especially 73-80).

Amundson then adopts Alberch's morphospace model and the problematic that follows: how are we to explain all the empty regions of morphospace and the fact that those regions that are occupied are clustered? (Amundson 1994, 561) "Birds and mammals cluster separately with open space between the clusters; so do felines and canines, and plants and animals." (562) Why? What leads to the clustering? For a "developmentalist," (Amundson's term), the search is for the particular mechanisms responsible for the growth and maturation of the organism that lead to the morphological discontinuities and the clustering. (564) Depending on the kingdom and phyla, these mechanisms range from patterns of gene expression, cell division and protein folding to gastrulation, neurulation, the formation of cell types, morphogenetic fields and so on. (see also my Chapter Three. More details to come in Chapter Five) The key for Amundson is that the developmentalist project is undertaken without any reference to adaptive value or natural selection, and this is no way inhibits its ability to explain what it seeks to explain: i.e. the origin and production of organic form. To make his point, Amundson chooses a favorite example of those fascinated by the morphology of living beings and the patterns of their production: the Fibonacci series seen in phyllotaxy.

II. Phyllotaxis, the Fibonacci Series, and Divergent Forms of Explanation

There are about 250,000 species of higher plants. And although the size, shape, and color of the leaf structures offers a spectacle of startling diversity, there is also a striking uniformity at work. Despite the variety of leaf shapes, there are basically only three ways in which the leaves are arranged on the stem: they can be opposite one another, whorled, or spiral. (Goodwin 1994, 116-7) The term "phyllotaxy" refers to these different arrangements of leaves—or bracts or florets--on plants. A fascinating feature of spiral phyllotaxis--the most prevalent form of arrangement--is that it correlates with the Fibonacci number series. In this series, each new number in the sequence is the sum of the preceding two: 1, 1, 2, 3, 5, 8, [...] 55, 89, 144...) This same pattern characterizes such diverse forms as the "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." (Amundson 1995, 565)[87] Plant ontogenesis often starts with a low numbered Fibonacci pattern (e.g. 3/5) and then transfers to higher numbers (34/55, 55/89) in larger and later stages.

The absence of patterns of growth that are divergent from the Fibonacci series pattern, either within or between species, "strongly hints at a constraint." (Amundson 1994, 565) Selection requires heritable variation and there just isn't the kind of continuous variation in evidence that the adaptationist perspective would expect. But might this growth pattern be an adaptation that has been fixed by stabilizing selection (as Maynard Smith et al. might argue)? Its uniformity across different species facing very different selective pressures in divergent environments makes this unlikely. But two forms of adaptationist explanation have been offered.

Another aspects of Fibonaccian phyllotaxis that intrigues observers is that it converges on an irrational angle measuring about 137.5 degrees.[8] The odd particularity of this angle stoked the imaginations of adaptationists, and one pointed out (C. Wright) that "If there were successive layerings of radial vectors about an axis distanced by the golden section, no vector will ever overlap a lower vector." (Amundson 1994, 565) In other words, in the case of a plant with spiral phyllotaxis, no higher leaf would ever be placed

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[87] "Particular phyllotactic patterns are associated with fractions in which the numerator and denominator are successive numbers in a Fibonacci series. The denominator indicates the number of leaves between successive exact overlaps as the leaves spiral around the stem. The numerator indicates the number of circuits around the stem before the overlap occurs." (Amundson 1994, 565)

so as to exactly shade an already existing lower leaf. This would seem to be optimal relative to the demands of photosynthesis which requires that leaf placement maximize the amount of light that can strike the surface. (565)[88]

With the preceding case, it would seem that the adaptationist program has been carried out "to the letter," and successfully so. A trait has been isolated and identified, its properties noted, and a story told to explain how the particularity of its properties contributes to the reproductive success of the class of beings under examination. How might a developmentalist respond?

Amundson draws upon the work of G. J. Mitchison to forward such an explanation: "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." (Amundson 1994, 567) Why? Because such proximity would interfere with the *growth pattern*, and the structure might become unstable. For a developmental-structuralist account, the next step is to identify the cause. Here the developmentalist seeks to identify an inhibitor mechanism to explain the size of the spacing between the leaves. (567) The size and number of the Fibonacci pattern is then explained by the rate of growth of the stem's apex. (568) More developmental details pile up on patterns of cell growth and division, energy requirements, and so on. Upon further research it turns out that "phyllotactic pattern is developmentally conservative, insensitive to environmental variables and varies among species in a discontinuous manner." (566) Not only does this give good ground for considering the pattern to constitute a kind of

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[88] It is also worth noting that the Fibonacci series leads to a logarithmic spiral which is the only curve that does not change its shape as it grows in size. (Gould 1980, 41)

(developmental) constraint, but it also perfectly meets the expectations of process structuralism: developmental integration and discontinuity in morphospace.

So which explanation is "better"? Upon further research, it was determined by adaptationists that the ubiquitous angle of divergence (137.5 degrees) had "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." (Amundson 1994, 565) Also,

> 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. (Amundson 1994, 566)

So how is the specificity and generality of the 137.5 angle of divergence to be explained? And how might an adaptationist respond? None is forthcoming according to Amundson's reading of a variety of practitioners within that paradigm on this subject. The Fibonacci pattern doesn't seem to have an adaptive value, and even more crucially, such a developmental-morphological scheme doesn't seem to interfere with a plant's ability to become adapted. Indeed, for adaptationists such as Stephens and Krebs, *these fixed patterns of phyllotaxis are not constraints*. Furthermore, phyllotactic pattern is no longer an explananda if it has no adaptive value. (Amundson 1995, 568) For an adaptationist, relatively fixed developmental patterns are only *constraints* if they cause a trait to be suboptimal. In their efforts to survive and reproduce, plants are especially sensitive to temperature and the availability of water and light. As these factors vary, many features of plants are modifiable so as to meet varying demands posed by different environments. Varying the size, shape, structure and thickness of leaves enables such organisms to adjust to varying environmental conditions. If the Fibonacci pattern does not interfere with such adaptive variation—and this seems to be the case--then, despite its ubiquity, it is not a constraint.

Though Amundson seems to favor the developmentalist explanation of this morphological feature, he still stresses the divergent aims, and explananda, of each form of explanation. Adaptationists focus on fitness and the processes most directly associated with it and reproductive success. In the case of plants, such processes include photosynthesis, and seed production and dispersal. Developmentalists, however, focus on form. On Amundson's reading of developmentalist Mitchison: "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." (1994, 568) What Mitchison seeks to explain are the features of plant growth which generate the many different Fibonacci patterns and why non-Fibonacci patterns are rare. The aim is to identify the "laws of growth." (Amundson 1994, 568) Put another way, one may explain the contribution of some form to the fitness of the organism without explaining the mechanisms responsible for the generation of the forms and the particular similarities and differences with other forms. For developmentalists, then, the adaptive value of some form is secondary (569), and the impasse between the two forms of explanation may be too wide to cross.

III. Constraints on Form; Constraints on Adaptation

As we have seen above, for Amundson, developmentalists and adaptationists do not seek to explain the same object. Because of this, there is reason to qualify the use of the term "constraint" as it is employed by each. When adaptationists employ the term "constraint," they refer to some event or process that has resulted in a trait that possesses less adaptive value (relative to some selective regime) than if said event or process were absent. Such constraints are called "constraints on adaptation" or constraintsA. Thus, for an adaptationist, there are many forces or events that impinge on or inhibit the adaptive possibilities of various traits. Some result from the inherent limitations of materials (e.g. bones comprised of calcium deposits can only withstand so much stress), historical contingencies (the availability of calcium is time-space dependent), phyletic inertia (e.g. the retention of vestigial structures), and/or the capacities of particular developmental mechanisms (e.g. osteogenesis: the calcification *process* which transforms collagen into bone). (Gilbert 1999, 351-8). For Amundson's adaptationist, any feature or process that interferes with and lowers the adaptive value of a trait is a constraint. That is, if that feature or process were absent, the adaptive value would not be restored to its expected level.

Alternatively, developmentalists are interested in the ways in which the origin and production of form (not fitness) is constrained (constraints on form or constraintsF). Related to this understanding of constraint is Alberch's morphological-macroevolutionary problematic: why are certain regions of morphospace occupied and others are empty? Amundson sums up the differences between the two views in regard to the case of phyllotaxy and the adaptive demands associated with photosynthesis as follows. From the perspective of an adaptationist, an "unchangeable developmental pattern can count as a constraintA only if it irremediably reduces adaptation." (Amundson 1994, 567) Since the "limiting factors" associated with phyllotaxy discussed above can be compensated for, they are not constraintsA. Thus, as Amundson puts it, quoting Niklas, "phyllotaxy 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." (567) In sum, says Amundson, "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 constraintA no matter how deeply it is entrenched in the developmental program." (567) On the other hand, for a developmentalist, a developmental pattern is a constraintF only if it precipitates 1) the regular construction of certain forms; 2) causes certain variations of said form and not others (i.e. it is a strong "bias"); and/or, 3) it prevents the production of other kinds of forms (i.e. renders particular regions of morphospace inaccessible: e.g. six legged-tetrapods, unsegmented insects).

If one accepts this constraintA/F distinction as expressed in the above, some of the confusion seen towards the end of the Maynard Smith et al. (1985) essay—what I called the "tangle" at the beginning of this chapter--may be seen anew, and even cleared up. For Maynard Smith et al. (1985), selection could not be ruled out as source of many canalized traits and other so-called DC's. In other cases, non-selection induced constraints were not thought to be of much evolutionary significance. From the perspective of a Stephens and Krebs-style adaptationism, such ambiguity and/or skepticism is irrelevant. (To be sure, MS et al. are much more interested in selection than adaptation as such.) They focus not on what *causes* the constraint, but on its effect: that is, whether or not the constraint lowers the adaptive value of the trait. If some developmental mechanism has persisted over long stretches of evolutionary time, it should not be regarded as a constraint on adaptation simply because there has been no variation. Rather, it is only a constraintA if

1) it inhibits the adaptive value of the trait with which it is associated *and*
2) it prevents morphological adjustments of other traits to compensate for the anti-adaptive fixity of the constrained trait.

For a developmentalist, a mechanism is a constraintF only if it restricts the range of morphological variation of the feature. This is independent of the its adaptive value or its effects on the adaptive value of other features. For example, the previously discussed tetrapod limb would seem to count as a constraintF. However, it could be argued that the restriction on morphological variation may not be a constraintA insofar as the limb plan can be modified so as to meet several different regimes of selective pressures, from the salt water seas to prairie and mountaintop to freshwater rapids and the sky.[89] In this sense, fins, wings, claws, and so forth may be construed as "compensatory adjustments."

Thus, according to the adaptationist viewpoint as understood by Amundson and practiced by Stephens and Krebs, the macroevolutionary persistence of the tetrapod limb is of evolutionary significance only if 1) a modification of the basic limb plan would

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[89] There are cases where there is morphological stasis but the variation of the developmental mechanism involved (Raff 1996, 192-3, 250).

increase the optimality of the limb and the developmental mechanism is what is prohibiting this modification. And, 2) the developmental mechanism is preventing compensatory adjustments to other of its aspects (e.g. finger length, foot width, etc.) Again, persistence alone is insufficient for the establishment of evolutionary significance (as hindrance or constraint) from the standpoint of the adaptationist. On the opposite side of the explanatory fence is the developmentalist. For him or her, the adaptive value of the limb is beside the point, the persistence of the pattern and the lack of certain kinds of variation of it is sufficient to establish morphological evolutionary significance.

IV. Conclusion of Part One: the Impasse

In earlier discussions of developmental constraints, especially in my Intro and Chapters One and Two, adaptationism appeared to be posed to appropriate key aspects of developmentalist and structuralist programs. For example, Dennett's reverse engineering (RE) program granted that not every organismic feature is an adaptation and "lower level" explanations (e.g. MS#1&2) should be employed when warranted and available. Also, some adaptationists, including Dennett, claimed that something akin to the adaptationist RE is necessary for the discovery of particular developmental constraints. (CH2, IV.5) If this is the case, then developmentalists require adaptationists to properly identify the phenomena which only they can explain. That is, only adaptationism is able to notice to the suboptimality of some trait. Such suboptimality indicates a constraint may be operative. At this point, the developmentalist is called in. Amundson's account, however, posits a different sort of relationship between the two camps, and constraintsA and constraintsF in particular.

Given Amundson's account, the key question for those interested in the role of ontogeny in the evolution of morphology is the following: under what conditions does a constraint on form lead to a constraint on adaptationism and how can that be determined? Amundson argues,

> a constraint on potential adaptation will only occur when the variant which is prohibited by the constraintF *would be* selectively favored if that variation were to exist. That is, whether a constraintF gives rise to a constraintA depends on whether the environment would selectively favor forms *forbidden* by the constraintF over forms *permitted* by the constraintF [emphasis in the original]. (Amundson 1994, 569)

The problem with this formulation is that, according to Amundson, naturalistic observation will never meet the conditions it demands because "the variation required for observable differential fitness is absent by hypothesis." (Amundson 1994, 569) For example, in the famous case of the tetrapod limb, comparing the adaptive value of the actual situation of possessing a single proximal bone (humerus, femur) with the adaptive value of double proximal bone—which has never existed and is "probably prohibited" given the production processes involved in the construction of the limb—seems exceedingly difficult precisely because no empirical assessment is possible. (569) This sort of methodological difficulty is of a different order than those discussed in Maynard Smith et al. (1985). In that essay, the problem was identifying the *cause* of the constraint (selection or developmental mechanism). Yet, even with the acknowledgement of such empirical difficulties—and combined with those already noted by MS et al.--Amundson argues there are still good theoretical reasons for believing that developmental processes constrain adaptation. His reasons for this, however, are different from all those encountered so far, except for Alberch.

Darwinian evolution is traditionally said to involve two stages, the production of (heritable) variation followed by the action of selective pressures. The latter is supposed to winnow down or sort traits based upon their contribution to the reproductive success of the organisms that possess them. (Wagner and Schwenk 2000, 197-203; Arthur 1997, 218-26; Whyte 1965, 42) As the story goes, the "winnowing down" is done by external, environmental conditions—especially, competition for food, predation, parasitism/disease, climate, interaction with conspecifics and mate choice. (Arthur 1997, 219). For Amundson, like Alberch and anyone who adopts this two-stage view, DC's obviously occur in the first stage, during the production of the phenotype. Following the familiar phraseology of Maynard Smith et al. (1985), developmental constraints "bias" that production. Thus, for the developmentalist, what is of interest is not merely the frequency and amount of variation that occurs, but the *range* of variation. (Amundson 1994, 570) That is, there might be much variation in regard to length of vertebrate digits, but what is of interest to the developmentalist is the range in which this variation takes place, not just how often any manner of variation occurs. For example, there is a wide range in overall digit length, but for individual digits the range differs and there is *infrequent* variation in *relative* digit length: e.g. in tetrapods, the middle digit is never shorter than the adjacent ones.

In sum, one of the phenomena that most interests the developmentalists is the range and patterns of variation. This is understood as "restrictions on the production of form" independent of adaptive value, hence the importance of morphospace studies and the evolutionary significance, and controversy, of the distinction between occupied and unoccupied regions of morphospace. Adaptationists, on the other hand, focus upon the fitness differences found among the variants; hence the importance of adaptive landscapes. But, as Amundson argued above, "the discovered facts concerning the embryological development of form imply nothing about the fitness relations between that form and its eventual environment." (570-1)[90] Again, the gap between the modes of explanation arises. For Amundson, the research programs of developmental biology, just like that of climatology, can be conducted in isolation from the questions of adaptation (571).[91] The impasse remains.

PART TWO

V.1 Options to the Impasse:

Amundson then outlines three possible positions one might take in regard to the possible interrelationship between development and adaptation:

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[90] Amundson doesn't raise the issue as to whether there are selective pressures on the embryonic processes independent of the adaptive value of the traits that they produce. This issue will be taken up in the next chapter in regard to Whyte and Arthur (1997).

[91] This is a fascinating though somewhat precarious claim especially insofar as aspects of the climate--such as atmospheric composition--are produced by organisms! (Margulis and Sagan 1986, 99-114) For the most part, such considerations are outside the scope of this dissertation, though some relationships between development and ecology will be addressed in Chapters Five and Six.

Neutralism: For a constraintF neutralist, Darwin's "conditions of existence" (selective pressures) aren't so strong or demanding; therefore, there "would presumably be room for "purposeless" conservation of pattern just as there is room for 'purposeless' variation and drift." (Amundson 1994, 571) Thus, much of the time, constraintsF may not result in constraintsA: "some selectively neutral traits might be present in a species because they drifted to fixation, others because they are products of a DC. Neutralism is true of both sorts of traits, but drift only explains the first." (571) Put another way, Maynard Smith et al. (1985) claim that there just are not that many developmental constraints, and that the ones that do exist are not significant relative to understanding the evolution of form. A constraintF neutralist makes the same kind of claim, *but in regard to selective pressures*. Some forms are adapted, but many are not, and the nonadapted forms *may* set the stage for the range of adaptation that occurs. (Amundson 1994, 571) This view is *consistent* with Alberch, but is not explicitly held or developed by him.[92]

Soft Adaptationism: argues that all organic traits have adaptive values, thus natural selection operates upon them all, but DC's determine the range of variation. For this reason, a constraintF is probably a constraintA. (Amundson 1995, 572)

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[92] "Neutralism" could fit nicely with the process structuralist perspective but this position is not held by those involved in the debates over DC's and developmentalism and structuralism. As such, I will not take a position on it nor discuss it in any detail.

> **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." (Amundson 1994, 572) For this "hard adaptationist" view, "Any developmental constraint can be (and have been) overcome by the forces of natural selection." (572) This last view can be seen amongst neo-Darwinians from Dawkins to Dennett.

Though one might think that Amundson leans towards the first or second view, he actually does not find any of these options satisfactory, mainly because none of them takes development seriously enough. Indeed, relative to the many positions discussed so far in this dissertation, Amundson is perhaps the most developmentalist. This can be seen in particular in regard to the manner in which he draws upon the work of Alberch.

V.2 Amundson and Alberch

As noted earlier, Amundson, contra Stephens and Krebs, argues that the AP is not necessary for detecting developmental constraints since the clustering patterns in morphospace are determined independent of adaptive value, suboptimal or otherwise. Furthermore, the "forbidden morphologies of digit patterns are determined not from surveys of digit patterns which actually occur in nature, but from a knowledge of the developmental processes that build those patterns in nature. " (Amundson 1994, 574) This point has been established previously, but Amundson goes on to unpredictably add,

> It is mistaken to infer the *lack* of a constraintF from a high degree of adaptation in an organism, and it is mistaken to infer a *reduction* in adaptation from the existence of a constraintF [my emphasis]. (Amundson 1994, 573)

In the above. Amundson emphasizes two distinct points: 1) The adaptive value of a trait might be limited for non-developmental reasons; 2) not only are constraints on form separable from constraints on adaptation, but a constrained morphology does not necessarily interfere with adaptive value. The second is crucial for this dissertation since it opens up the notion that constraints may not impede the adaptive process but perhaps even contribute to it. (This notion of positive constraints will be pursued in Chapters Five and Six.) The preceding is perhaps Amundson's most novel contribution to the debate over the significance of developmental constraints in contemporary evolutionary theory. Developmental mechanisms are what make adaptation possible in the first place. That is, it is not just that developmental mechanisms *permit* certain adaptations to occur, they *produce* them. In this sense, the developmentalist form of explanation is a necessary part of the full explanation of some trait. (1994, 564-5)

Because of its brevity, however. the example of a "positive constraint" that Amundson gives is somewhat vague if not confusing: "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" (Amundson 1994, 573). First off, it would seem that Amundson is referring to "correlated progression" here, not the "correlation of parts." The correlation of parts, known about since before Darwin, is often cited as an example of a developmental mechanism's interfering with adaptation, not enabling it. That is, if characters A and B are linked ("correlated") because they share a developmental mechanism at some point during the ontogeny of each, then changes in A will lead to changes in B. Although selection may be able to successfully increase the adaptive value of trait A, the adaptive value of B could decrease. If B's adaptive value is actually lowered, then the developmental mechanism would be considered a constraintA. Given the frequency with which genes play a role in the production of many different phenotypes, this is not a rare occurrence.

Yet, Amundson seems to be referring to what developmentalists call "correlated progression." Correlated progression is said to occur when changes in one element of a embryological region induces changes in other elements. For example, in vertebrates, a change in the skeletal cartilage will likely bring about a change in the placement of muscles and nerve axons since the cartilage informs the muscles and induces the placement of nerve axons. Similarly, in the case of the transition from reptiles to mammals, there were coordinated changes among jaw structure, jaw musculature, tooth deposition and shape, the cranial vault, and ear. All these changes are thought to be a consequence of the enlargement of the braincase which freed up other elements to "migrate." (Gilbert 1999, 896) In both of these cases, even if a selective pressure initiated the changes (by favoring a larger skeleton or brain case), selection did not determine the range of features affected. The linkage is developmental. Nor is it the case that selection orchestrated the coordination of this dramatic morphological transformation: for this to be true, selection on each individual feature would have been necessary. This was not the case. (Alberch 1982b, 313)

Amundson notes that in the cases above, the developmental constraints are what enable the lineages in question an evolutionary opportunity to switch modes of life, e.g. from reptile to mammal. (Amundson 1994, 574) That is, the morphological transformations were "unintended" side-consequences of selection "aiming for" the adaptive improvement of a single feature. In this sense the DC is "positive" or "creative," a source of evolutionary novelty. This position was noted in regard to Alberch in Chapter Three and Newman and Muller in the Intro. It is further addressed in Chapter Five and especially Chapter Six in regard to Resnik (1995) and Gould's "cross-level spandrels" (2002).

This critical insight is often missed by adaptationists and much of contemporary evolutionary biology because, argues Amundson, there is a tendency throughout the literature to see development as either under the direction of selection or as that which impairs optimal adaptivity. As he puts it,

> classifying developmental constraints as constraintsA has a second pernicious effect. It trivializes the detailed causal understanding which developmentalists believe is essential to evolutionary biology. [...] For Dawkins and others who black box development, detailed knowledge of development isn't necessary for the same reasons that a detailed understanding of earthquakes, hurricanes and ice ages isn't. (1994, 574-5)

As discussed before, the underlying genocentrism of the adaptationist approach combined with its tendency to treat the organism as a set of discrete traits continues to undermine the significance, and range, of the evolutionary contribution of developmental processes.

It is my contention that what Amundson is trying to get at, but does not fully articulate, is the sense in which developmental constraints are *productive*. This is true on a number of different levels. First, a rather rudimentary point. A process of any kind is not a set of random movements, it is, rather, a sequenced set of constrained motions and/or transformations. (A completely unconstrained set of motions would merely involve objects randomly bouncing off one another, destroying each other, or never even coming into contact.) This is true of all physico-chemical processes, and it is even more true of developmental ones. It is because of the restrictions on such movements and their further coordination that something new emerges. Thus, it is trivial that developmental mechanisms are "constrained." All mechanism are constrained. Endless modifiability would lead to the disintegration of the mechanism. When these (constrained) processes impair the adaptive value of traits, adaptationists call them developmental constraints (constraintsA), and when they restrict morphological variation, developmentalists call them constraintsF. However, it is precisely because these processes are constrained that adaptation is at all possible.

Here, we have awkwardly and incompletely stumbled upon an issue central to the next chapter: what kind of system needs to be in place in order for adaptation to occur? An organism is a kind of system which is able to withstand certain kinds of modification without falling apart. As discussed in the Intro and Chapters Two and Three, it is a nested set of hierarchically arranged components and processes that wards off some kinds of change while it permits others. Returning to the example above, reptiles still must be able to eat as there jaws change. This is what is called a "functional constraint." (Schwenk and Wagner 2000) The same is true in regard to the production of these traits: the change in the production of the skeletal cartilage cannot be of the type that inhibits the processes responsible for the formation of the braincase. This level of articulation is missing in Amundson and for the most part Alberch, but its articulation is consistent with their approaches.

Amundson concluded by arguing that "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." (1994, 573) However, it is not entirely clear what those resources are nor how the integration of development into evolutionary studies should take place. An additional problem is that some, if not many, of the criticisms leveled in this essay do not hold up against adaptationists like Dennett who do not black box development but instead integrate it within an adaptationist perspective (see my Chapter Two on Dennett's "reverse engineering" approach.)

V. Conclusion to Chapter Four: Where to?

> Identifying different explanatory projects only partially resolves the relations between different domains of biology. For while these projects are distinct, they are not independent. Our views on development, for example, affect our views on evolution, and vice versa." (Sterelny and Griffiths 1999, 50)

Amundson helpfully lays out how the projects of evolutionary theory and developmental theory differ in regard to their explanans and explanandum. Also, the claim that inferences cannot be drawn from constraintF to constraintA is important. Although he does go further than previous view discussed in calling for a Developmental Synthesis, it is not clear what this synthesis would entail, nor does he does note existing adaptationist attempts at such a synthesis. These can be seen in rudimentary form in Dennett, and more fully developed in Raff (1996), Gerhart and Kirschner (1997), Hall (1992), and Arthur (1997.) This issue and the ones directly following are the subject of my next chapter. Also, he seems to adopt the two-stage model of evolution where developmental processes do the producing of forms but natural selection does the selecting and testing of them. Yet, if the developmentally relevant part of the environment is noted, this distinction is not so hard and fast, or at least the internalist/externalist aspect is not so strong. This point can be made from an adaptationist perspective: developmental processes themselves are subject to selection, or from one which is neither genocentric nor adaptationist, as in the case of Developmental Systems Theory.

What is also intriguing about Amundson's constraintsA/F distinction is that, to some extent, it replays the old distinction between functional and evolutionary biology. As Ernst Mayr famously characterizes the two sides of this methodological disjunction, functional biology (e.g. physiology, molecular biology, embryology) seeks to explain those causal mechanisms ("proximate causes") which are involved in the production and function whereas evolutionary biology ask the "what is it for?" questions which drive the adaptationist program. (Mayr 1989, 68-71) Thus, just as geology seeks to explain the formation of sedimentary rock by understanding the processes that sort and layer elements according to their respective weights and sizes and so on, developmental biology explains the formation of bones via an understanding of the transformation of mesenchymal cells into cartilage and the calcification of the cartilage into bone.

So how then to construct the synthesis? It is easy to see how it is to be done—and has been done—from the adaptationist perspective: include developmental studies so as to explore how such processes are subject to selection and interfere with the optimality of trait production. But Amundson says that "advocates of a Developmental Synthesis are asking for much more than a mere acknowledgement of adaptive imperfection" (i.e. development as a set of constraints which impede selection's fine-tuning of traits towards optimality]. They want to integrate the complex and internal details of embryology into the study of evolution." (575) But if not a more developmentally detailed version of Dennett's "reverse engineering" perspective, then what?

CHAPTER FIVE:

PART ONE OF THE CONCLUSION: EVO-DEVO VS. DEVO-EVO; FUNCTIONALISM, DEVELOPMENTAL INTEGRATION AND THE LIMITS OF SELECTIONISM

I. Introduction

This chapter has two aims: first, to explore the claims that evolutionary developmental biology constitutes a response to Amundson's impasse by forging a "synthesis" between developmentalism and adaptationism. The second aim is to show that as the debate has evolved, the category of "developmental constraints" has continued to shrink although controversies concerning their significance continue. I will argue that in regard to claim one, there is no synthesis, but many cross-fertilizations that have resulted in two competing views: an adaptationist "appropriation" and a process structuralist "divergence." As for claim two, I shall argue that there are some positive aspects to the narrowing of the notion (such as the operationalization of the term), but the negative aspects outweigh the positive. In addition, operationalizing the term can be achieved without most of the "narrowing."

One aim of this chapter is to argue that calls for a "Developmental Synthesis" are misplaced. There is no one obvious, noncontroversial synthesis that lies waiting to be realized. Rather, from the perspective of development and evolutionary morphology, there are, at least, two actually existing configurations: selectionist evo-devo and process structuralism. While the former, deservedly, draws more and more attention, the insights, concepts, and aims of devo-evo are wrongly at risk of being devoured by evo-devo. In order to get at this divergence of views, I draw upon a short essay by evo-devo co-founder Brian Hall appropriately entitled, "Evo-devo or Devo-evo, does it matter?" (2000). I will argue that there is a difference between these two hyphenated hybrids, and yes, the sequence of the hyphenation does matter. Furthermore, I shall argue over this chapter and the next that, at least for the near future, the divergence and opposition between the two research programs should be preserved. In sum, eight years after Amundson's call, there are many cross-fertilizations but still no "synthesis." And this is not such a bad state of affairs.

The second aim of this chapter is to show how the notion of developmental constraint continues to be defined more narrowly as adaptationist and/or selectionist approaches pick up developmentalist concepts and themes. While this narrowing started with MS et al. (1985), it has accelerated since the mid-1990s. While cross-fertilization among different camps has been productive--e.g. Schwenk's notion and study of functional constraints and evolutionarily stable configurations—other concepts (e.g. "internal selection" and "coadaptation") are innovative but oftentimes either misleading or misapplied.

The second half of this chapter examines how recent practitioners in evo-devo have departed in subtle ways from the previous debates over DC's. Key to this departure are the notions of internal selection, coadaptation, (Whyte 1965, Arthur 1997) and Evolutionarily Stable Configuration (Schwenk 2001, Wagner and Schwenk 2001, Schwenk and Wagner 2001). Over the last 5-10 years, I argue that evo-devo has offered adaptationist and/or selectionist explanations of many of phenomena previously though to fall under the category of developmental constraints. It has done this by transforming elements of the process structuralist position and redefining and widening the scope of selection. Key to this maneuver has been the further articulation of stabilizing selection and Arthur's (1997) resurrection of the notion of internal selection first developed in Whyte (1965). This concept is developed further and, helpfully, applied more narrowly by Schwenk and Wagner. I conclude by arguing that these three concepts have carved out and creatively articulated a relatively "internalist" middle ground between adaptationist attempts to explain organismic morphology in terms of (external) selection and process structuralist attempts to account for evolutionary morphology in terms of fixed developmental mechanisms. It appears that such a view does not fit comfortably on either side of Hall's disjunction since it appropriates contributions made by process structuralism

II. Evolutionary Developmental Biology

One bridge across Amundson's impasse has been constructed by adaptationists interested in explaining the developmental integration of organisms. Adaptationism is all about the explanation of the evolution of characters and the reasons why they become dominant in a population. Evolutionary developmental biology, or "evo-devo," has shown that simply identifying nucleotide substitutions alone cannot explain such change, nor can the simple registering of immediate selective pressures.

Like developmentalists and structuralists before them, the mission of evolutionary developmental biology is to explain the following three sets of phenomena: the persistence of body plans and phylotypic stages, the emergence of new traits and the origination of body plans, and the macroevolutionary patterns of morphological change.

In order to explain these phenomena, evo-devo aims to determine the pattern of phylogenetic variation in 1) developmental pathways and 2) their underlying genetic architecture. (Gerhart and Kirschner 1997; Raff 1996; Arthur 1997) Phylogenetic pattern then includes not only the taxonomically high-level trends at the phenotypic (e.g. morphological) level and the origination of body plans but the "variation in the degree to which the genetic architecture of development is *hierarchically* (and otherwise) organized." (Arthur 1997, 83) The following are examples of questions driving research in evo-devo:

1) How do developmental mechanisms and their genetic control systems map to the phylogenetic tree of descriptive ontogenies?
2) What does this mapping tell us about sorts of mutational changes (and consequent cellular mechanism changes) involved in the evolution of development?
3) What implications, if any, do data collected to answer questions 1 and 2 have for the mechanism of spread of the new variant ontogenies at the population level? (Arthur 1997, 84)

The specificity of these tasks/questions make concrete what *a* supposed "developmental synthesis" looks like when operationalized into a research program. For example, over the last ten years, there has been much research into Hox genes. Such gene complexes are thought to play a key structural and regulatory role in the development and evolution of major morphological aspects in arthropods (i.e. *Drosophila*) and vertebrates. (Raff

1996; Gilbert 1999, 635-45) This case is an example of a study which seeks to explain "high-level evolutionary trends" such as the anterior-posterior axis, segmentation, and appendage formation via the causal role of specific elements in the genetic architecture.

III.1 Syntheses: Evo-devo or Devo-evo?

Brian Hall, one of the major figures in evolutionary developmental biology (Arthur 1997, 86), recently penned a short editorial (Hall 2000) in which he sized-up evo-devo's ability to answer the questions posed above and cautiously, and critically, peered ahead. Though the piece is brief and a bit tenuous, it provides an effective means for assessing certain differences among those concerned with the relations of and cross-fertilizations between evolution and development. One topic which dominates the piece is the manner in which evo-devo has forged a "Synthesis," Hall's term, between evolutionary and developmental biology and the difficulties and controversies that have come with such efforts—not to mention outright resistance of those who still oppose developmentalism in any form. As his title "Evo-devo or devo-evo—does it matter?" indicates, Hall provocatively implies that a different Synthesis might have emerged, and could still. But, it has not and, he believes, for good reason:

> Evo-devo is a synthesis of evolution and development with emergent properties not found from analysis of development or evolution alone. Devo-evo would see the current theory of evolution (the neo-Darwinian synthesis) as incomplete and seek to modify it, or even replace it, with a theory *grounded in development* [my emphasis]. (Hall 2000, 177-8)

Clearly Hall, like many others (Raff 1996, Arthur 1997), sees evo-devo as a critical effort to *fill in a serious gap* faced by evolutionary biology since the Modern Synthesis and the subsequent dominance of population genetics and "hard" adaptationism. As this dissertation has argued over the last four chapters, it is now more widely accepted that one must seek to understand the many levels of ontogenetic processes in order to explain the relationship between genotypic and phenotypic change. This is contra Lorenz and the early Dawkins (1976, 62) for example.[93] However, for most, evo-devo is an "enhancement" and/or a completion, not a "revolution." The reason for this, Hall claims, is that there is no overturning of the central tenets of "neo-Darwinism." (2000, 178) Therefore, although evo-devo has produced knowledge not found from analyses of evolution or development alone, adaptation remains the central concept and selection the chief factor for explaining complex adaptations and evolutionary morphology. Although debates over the unit of selection and the mode of inheritance rage on,[94] the primacy of selection as an evolutionary force is not challenged. What is hotly contested is how, and on what level, it operates.

Then, surprisingly, Hall goes on to claim,

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[93] The succinctness and popularity of the remark make it worth citing: "The details of the embryonic developmental process, interesting as they may be, are irrelevant to evolutionary considerations. Konrad Lorenz has put this point well." (Dawkins 1976, 62)

[94] Hall concludes, however, by stating it may be necessary to invoke modes of inheritance other than transmission of genes (2000, 178) That jury is still out, as is an understanding of "how variability in developmental stages coexists with the stability those stages and processes exhibit across animal ontogenies;" and "whether cells, cell condensations, or embryonic fields should be added to genes and phenotypes as units of evolution subject to selection." (178)

> *While it is difficult to imagine what a developmental evolutionary biology [devo-evo] would be*, it would not place primary emphasis on genes as the only units of evolutionary change [my emphasis]. (Hall 2000, 178)

True, a devo-evo would not be genocentric, but why is it so difficult to imagine, especially since it already "exists"[95]? As with other earlier adaptationist appropriations of developmentalist themes and concepts, I believe there are three philosophical reasons for evo-devo's inability to even recognize a devo-evo: 1) devo-evo's anti-genocentrism, as noted by Hall, 2) the claim that developmental mechanisms and/or DC's may play significant negative and "positive" and creative evolutionary roles; 3) that ontogeny is hierarchical in a non-genocentric manner. As has been seen over the course of this dissertation, even as adaptationism has become more developmentalist, it has had difficult accepting and/or recognizing the significance of the preceding three claims.

An effective means for understanding the split between evo-devo and devo-evo is to look at the recent evolution of the debate over constraints and its current status. The debate over constraints was crucial for developmental biology's (re)entry into evolutionary biology (Gould and Lewontin 1979, Raff 1996) but determining their ontogenetic cause and evolutionary significance has been controversial from the start. This is especially evident when considering two "early" essays: Gould and Lewontin's

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[95] The actuality of "devo-evo" is a bit more complicated than I suggest above, especially since there are significant sociological and financial aspects to be considered. Though I believe that I have developed a coherent and operational process structuralism drawing up a range of work, there is not necessarily a group of practitioners who self-identify as "process structuralists" or "developmental" evolutionary biologists.

(1979) and Maynard Smith et al.'s (1985)[96]. Although both are of significant influence (Sober 1993, 142; Sterelny 1996, 196; Schwenk 1995 251) for contemporary practitioners, each is oftentimes superficially cited with no real examination of the controversial complexity of the debates involved and the positions taken. This is one reason for the detailed analyses of these essays in Chapters One thru Three.

The importance of Gould and Lewontin's view for the present discussion is that their taxonomy of constraints, though flawed, is bound to a distinctly process structuralist theoretical approach. This approach frames their taxonomy and leads to the positing of an alternative theoretical and research model to the "adaptationist paradigm."[97] Their alternative is the *Bauplan* paradigm. (CH2) They did not consider this view to constitute a "revolution" because it draws upon a rich tradition, one that is also recognized by current practitioners of evo-devo (Raff 1996, Hall 1992, Arthur 1997) However, given Hall's disjunction, the *Bauplan* paradigm would fall on the devo-evo side because of its strong criticism of and challenge to adaptationism and selectionism combined with its emphasis on physico-chemical and self-organizing processes which were never subject to selection. Such an approach and paradigm are significant because, even if problematic, they at least provide a picture of what a devo-evo might look like, and offer: that is, its concepts, form of explanation and criteria for determining evolutionary significance.

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[96] It is worth recalling that the full list of authors includes some process structuralists and forerunners of evo-devo, but do not appear to shape the much more selection-oriented conclusion. The full list of authors is John Maynard Smith, Richard Burian, Stuart Kauffman, Pere Alberch, J. Campbell, Brian Goodwin, R. Lande, D. Raup, and Lewis Wolpert.

[97] Again, Gould and Lewontin define the adaptationist paradigm as the view that organisms are sets of traits and the existence of each trait can be explained in terms of ability to meet the demands posed to it by some environment (particular selective pressures). (Gould and Lewontin 1979, 73)

Indeed, there are those who have sought to develop just such a view. The many works of Alberch, Amundson, Goodwin, Webster and Goodwin, Depew and Weber (1995), and Newman and Muller among many others have all aided in the articulation of a process structuralist account. Yet, despite the influence of Gould and Lewontin (1979), the subsequent debate over developmental constraints did not proceed along process structuralist (devo-evo) lines as my discussion of MS et al. made clear. That is why I had to bring in Alberch. But what about more recent views of DC's that have had the chance to witness and benefit from the rise of evo-devo?

III.2 Two Contemporary Approaches to Developmental Constraints

Two more recent views on the developmental constraints debate give us a more up-to-date picture of how a taxonomy of constraints might be set up given the existence of evolutionary developmental biology as a research program and discipline.[98] Towards this and other ends, I shall discuss the views of Resnik (1995) and Schwenk (1995). My reasons for selecting these two are twofold. First, taken in tandem, Resnik and Schwenk are both comprehensive and divergent enough to cover a wide range of views found within the debate. Also, although both, in different ways, remain in partial continuity within MS et al., they also push the debate further than their predecessors. I have chosen each one in particular, however, for different reasons. Resnik's (1995) is widely cited and comprehensive though not all that friendly to those working in evo-devo or devo-evo, despite a link to Gould. Indeed, it explicitly leans toward the neo-Darwinian camp.

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[98] Three of evo-devo's major works appeared well after Maynard Smith et al.'s (1985) essay: Hall (1992), Raff (1996), Arthur (1997).

(Wrongly, I shall argue.) On the other hand, Schwenk's (1995) taxonomy directly connects to two key concepts in evo-devo: "evolutionarily stable configurations" (Wagner and Schwenk (2001), Schwenk (2001), Schwenk and Wagner (2001)) and "internal selection" (Whyte 1965, Arthur 1997). Also, the latter's taxonomy is, I will argue, comparatively more innovative and comprehensive than Resnik's. The essay proceeds as follows: Resnik's taxonomy and its problems; Schwenk's taxonomy; internal selection, coadaptation, Evolutionarily Stable Configurations (ESC's) and the relevance of the evo-devo/devo-evo split.

IV.1 Resnik's Taxonomy of Constraints and Its Problems

> The notion of a developmental constraint is important in understanding how development influences evolution; the notion of a developmental pattern is important in understanding the evolution of development. (Resnik 1995, 3)

Resnik continues in the tradition of Gould and Lewontin and Maynard Smith et al. but further refines the taxonomies of each. Whereas Gould and Lewontin distinguished among phyletic, developmental, and architectural and Maynard Smith et al. constructed a fourfold distinction within developmental, Resnik offers a different approach which draws on, but is critical of both.

Like Maynard Smith et al., Resnik's focus is entirely on "developmental constraints." There are three sets of criteria by which developmental constraints can be classified: local/universal; ahistorical/historical; and passive/active. The local/universal distinction distinguishes among constraints in regard to their taxonomic *scope*. Local and universal represent ends on a continuum, thus we can speak of constraints that are "more universal" or less local and so on. This distinction is equivalent to that found in Maynard Smith et al., but it is not made in Gould and Lewontin (1979). (CH3, III.1)

The ahistorical/historical distinction is also congruent with Maynard Smith et al. *Ahistorical* refers to those factors which are independent of the contingencies of biological evolution. Ahistorical constraints includes laws of nature and all those explanations found in the disciplines of chemistry, physics, aerodynamics and so on insofar as the latter too are universal from the perspective of biological history. *Historical* constraints are the product of biological evolution itself. If the course was different, the product might not arise again. Gould (especially 1989b) is among the most prominent defenders of the importance of such factors (which is why in these last two chapters I will classify his process structuralism as "historicist"), but nearly all others recognize them as well. Gould and Lewontin (1979) called such constraints "phyletic," and Dennett calls them "frozen accidents" (1995, 199). Resnik offers a useful nonbiological example to distinguish between the two kinds. In automobiles, the internal combustion engine is a constraint on car design, but other modes of propulsion were and are possible. However, no matter the engine type, all cars must conform to the laws of aerodynamics and many design decisions are based upon the demands set by such ahistorical factors. (1995, 5) Resnik names multicellularity as a constraint closer to the universal end of the scale and insect segmentation patterns as a more local constraint. Both are *historical*. Complex systems constraints (MS#2) are named by Resnik as ahistorical. (1995, 5)

Resnik's considerations of local/universal and ahistorical/historical are fairly consistent with MS et al., although he further specifies how to conceive "bindingness." Rather than worrying about how to understand just how *entrenched* a constraint is, Resnik focuses on the degree of difficulty of a transformation from one state to another. For such an undertaking Resnik offers the notion of "difficulty" which is defined by "the number of changes and the number of generations it takes to bring them about." (1995, 4) He goes on to offer an example,

> I suspect it would not require many changes or much time (on a geological scale) for us to evolve an extra finger on each hand, but it would take many changes and a great deal of time to for us to develop the capacity to photosynthesize. Of course there are bound to be some exceptions to this generalization, and it should only be viewed as a suggestion to guide further research. (Resnik 1995, 4)

I think this concept and both of these examples offer much more to consider than Resnik notes. Indeed, further contemplation of each may undermine the kind of research focus he recommends. For example, with the digit case, it is the range of the variation and the digit number that excites so much fascination. How many digits could be generated? At what point would other aspects of the limb have to be changed to accommodate such additions, or does the rest of the limb structure prohibit them as is more likely given the fact that seven or eight is the highest number of digits produced. (Hinchliffe 1994, 163) (see Ch6, II.2 for details.) In other words, it is the numerical aspect of "difficulty" that potentially misleads. How many changes involved for us to evolve five limbs? Given our bilateral symmetry, six might be less difficult. Indeed, possessing "five limbs" might be more towards the far end of the "difficulty" continuum with photosynthesizing mammals than with six digit humans. In any case, I would argue a notion of difficulty must take into account previous patterns of change and the range of variation and not just the "number of changes." Fifteen steps in one direction might be easier than two in another. This is one of the reasons for the morphospace diagrams.

Using Resnik's terminology one might be tempted to reply that consideration of the number of generations involved for each step could meet my challenge. Thus, Resnik's defender could allow that step 1-2 might take more *generations* than steps 5-16. But speed of change (number of generations) does not necessarily correspond to difficulty of change. In other words, "easy" changes would imply that few steps are required and no decrease in fitness results. But such changes might take *many* generations since the production of genetic variation is random with respect to phenotype.

I would argue that at least two more criteria are necessary to clearly define "difficulty": the net fitness increase or decrease resulting from each step relative to (external) selective pressures, and the effect on the (internal) developmental dynamic. I shall return to both of these notions when discussing Arthur's concept of "internal selection" below. In addition, Resnik's acceptance of the distinction between historical and ahistorical constraints will be put into question when I discuss Schwenk and Gould. Resnik's next distinction, however, is a big one for Gould and gets at a key issue for practitioners of evo-devo and the viability of process structuralism/devo-evo.

IV.2 Passive and Active Constraints

An often implicit distinction runs through the literature on constraints, especially among those who lean towards the devo-evo side of the ideological spectrum: the distinction between active and passive constraints. Resnik draws heavily upon the oft-cited Gould (1989a) to make his case for this most critical dichotomy.

In his essay on a developmental constraint in the land snail taxa *Cerion*, Gould (1989a) argues that some DC's do not merely *restrict* the action of selection, they *direct* the course of further evolution in a lineage. For Gould (1989a), the "negative" (his term) sense of constraint entails the "absence of variation for change in particular directions." (Gould 1989a, 518) This indicates the sense in which constraints are "restrictive." But there is another "positive" sense: constraints may direct or even force action in a particular way, "compelling or channeling phenotypic change in a direction set by past history or formal structures rather than *current* adaptation [my emphasis]" (518) In a sense, the constraint or set of constraints acts like a kind of template which *enables* a range of variation, but the range is bounded by the constraints which make it possible. Alberch too stresses such positive constraints (Alberch 1982, 313) as do Burger (1986), Wagner (1988), Goodwin (1994), and Gould (2002). (See also Newman and Muller (2001, 310).)

Resnik renames Gould's "negative" and "positive" *passive* and *active*. (I shall use Resnik's terms for the present discussion.) Such a distinction, he argues is akin to the distinction between background conditions and causal agents (Resnik 1995, 5-6) He writes, "Whether we cite a particular agent or set of conditions as the cause of an event depends on what we want to know about the event and what we already know, i. e. our interests and background knowledge."[99] (Resnik 1995, 6) The example he gives is of a forest fire. Background conditions would include hot and dry conditions, but the "causal agent" would be the unattended campfire which initiated the blaze. (6) The former are "passive," the latter "active." Resnik concludes his point by stating that developmental constraints are "active" only if there is empirical evidence that they function as "independent, causal mechanisms in evolution." (7) Their independence, from selection, is what potentially makes them a constraint from the standpoint of selection. Though Resnik does not address this point in detail, he does acknowledge that persistent developmental patterns do not necessarily constrain adaptation, as noted earlier by Amundson.

According to Resnik, neo-Darwinism (i. e. genocentric adaptationism) recognizes constraints that are local, historical, and/or passive but opposes any view which asserts that constraints are active in the sense spelled out above. (Ahistorical constraints neither confound nor impress and thus are not of much interest according to Resnik. I shall return to this issue when discussing Schwenk.) Resnik argues that in order to demonstrate that DC's are active, developmentalists "must either show that (a) we should not define evolution solely as changes in gene distributions; and/or (b) Weismann's doctrine is false." (Resnik 1995, 7) Interestingly, these criteria are similar to Hall's pronouncement about a possible devo-evo. That is, Hall argued that a devo-evo would reject genocentrism and Resnik argues that believers in positive constraints are also

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[99] For the moment I am skipping over this crucial epistemological point about the theory and/or context dependence of explanation in order to stay focused on questions of taxonomy. The epistemological point will be discussed later in the chapter in regard to Gould. It is worth noting now that Resnik distinction between active and passive constraints and the theory-dependence of explanation are both found in Gould (1989a) and (1980) respectively and are major topics in Gould (2002).

committed to an anti-genocentrism via the acceptance of either (a) and/or (b). Putting aside issues with Hall for the moment, obviously evo-devo accepts (a) and has offered much evidence to support this view. Indeed, such a view is part of the core of its theoretical and practical approach (see above critiques of population genetics and the Modern Synthesis in general).[100]

There are a number of problems with Resnik's view. First, many neo-Darwinians dispute the claim that developmental constraints are historical and passive in Resnik's sense. To cite one notable and previously discussed case, Dennett (1995) recognizes the importance of attending to the particularities of development, and he acknowledges that developmental processes may constrain the action of selection to shape morphology. But he does not regard them as significant from an evolutionary perspective. DC's for Dennett are moveable roadblocks: they may divert traffic for a period of time but if a real need (strong selective pressure) for this route arises, then the block is moved through the action of selection. or the lineage is eliminated. Passive DC's do not place *significant* limits on variation, nor do they in the long run restrict phylogenetic pathways. (Dennett 1995, 229-60) Following Maynard Smith et al. (1985), inertia resulting from the developmental embeddedness of past adaptations (Gould's phyletic constraints, Resnik's "historical" constraints) and stabilizing selection are more likely to restrict the range of variation. This is due in large part to the fact that selection has the ability to tinker with developmental processes, thereby overriding (or eliminating altogether!) persistent developmental patterns that interfere with the action of current selective pressures. The

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[100] However, as was noted with Hall, evo-devo seems not to endorse (b) although some recognize the possibility: those who lean toward the Developmental Systems Theory (DST) camp readily accept both (a) and (b). (Oyama, Griffiths, and Gray 2001, 4-5)

purpose of criticizing Resnik for what might appear to be a minor point is to emphasize that even "passive" constraints may be construed as a challenge in contemporary evolutionary theory. They are not mere "gap fillers" or "extensions" of the Modern Synthesis. As I have urged throughout this dissertation but especially in regard to Dennett and Maynard Smith et al (Chapters Two and Three), appreciating the evolutionary significance of passive DC's is still a real struggle for Adaptationists, genocentric or otherwise. Many, even Dennett!, have begun to note their existence but are unwilling to address their role as a factor shaping macroevolutionary patterns despite all the depiction of persistences.

In sum, Resnik offers a threefold taxonomy of constraints: local/universal; ahistorical/historical; and passive/active. The first is well-articulated and consistent with MS et al. and my own view. The second is well-founded but insufficiently addressed—it is given more adequate attention by MS et al. It will be discussed at length below and in the next chapter in regard to Schwenk and Gould's (2002). The third is articulately drawn but, as I argued above, the implications of this distinction are not accurately or adequately assessed. Put another way, and returning to a theme of this chapter, though the existence of active DC's goes a long way to insuring a viable devo-evo, their existence may not be necessary. I shall attend to and defend the notion of active constraints in the next chapter.

V.1 Schwenk's Taxonomy of Constraints: Patterns and Processes

The distinction between pattern and process is a major theme in Resnik (1995) and Schwenk (1995) and throughout evo-devo (Arthur 1997, Raff 1996) Schwenk moves

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the issue to the forefront in his construction of taxonomy of constraints which consists of two classes. "Class I" are macroevolutionary constraints or patterns as seen in the persistence of 35 or so body plans in the Animal Kingdom. This first class of constraints are best thought of as persistent patterns and represent the "channels" taken by evolution at the phylogenetic level and may even indicate the boundary conditions of future evolution. (Schwenk 1995, 253) Morphospace approaches—as in Alberch (1980, 1982a, 1982b, Alberch et al. 1979), (Arthur 1997) and Eble (2001), among many others) make evident such constraints through their depiction of occupied and unoccupied regions of morphospace. (see my section Chapter Two, II.1) Schwenk argues that studies of Class I constraints should not make presumptions about causality. Various kinds of selection or developmental constraint may be responsible for such stasis and/or "bounded" patterns of variation. Whereas Class I constraints are a category proper to the study of macroevolutionary morphology and the associated methods, Class II constraints are studied by all developmental biologists.

Class II constraints result from those processes responsible for the nonrandom production of variants. (1995, 253) This view harks back to Alberch and Maynard Smith et al.'s definition of a DC as a "bias" in the production of phenotypic variation. Also included here are genetic constraints including the lack of genetic variation and pleiotropy (i.e. MS#2). This conception is a *process* definition in contrast to Class I's *pattern* definition. (253) Class II definitions disallow the possibility that natural selection is a cause, even if it is the case that "at some level, selection builds and possibly maintains the developmental systems that bias phenotypic variation, thereby causing the constraint (e.g. Maynard Smith et al. 1985; Stearns 1986)!" (Schwenk 1995, 254)

Schwenk's reasoning here is in line with my own classification of phyletic constraints (canalization) as (selection-independent) developmental constraints since even though they arose for selective reasons they persist for developmental reasons. (CH3, VI.1; CH6, III.2)

Here I think Schwenk is differing with Maynard Smith et al.—even though he cites them as if they accepted his statement!--and many of those who are quick to invoke stabilizing and other kinds of selection to explain persistent or constrained processes. Part of the reason for this confusion goes back to Resnik's requirements for considering a DC to be "active": one can reject genocentrism (Resnik's conditions (a) and/or (b) stated above) and still deny that DC's are active. (Again, it is also true that many, wrongly, espouse genocentrism yet do not grant the significance of passive constraints.) One does this by accepting that in some cases DC's are emergent—not under the direct control of selection—but, given enough selective pressure, variation, and time, such constraints can be overridden or the lineage is eliminated for fitness reasons. This stance is explicit in Dennett and implicit in MS et al.'s conclusion (1985, 281-4), despite waverings within the essay (remember all the co-authors!). Strangely, given another passage in the essay, it even seems to be Schwenk's view,

> Given enough time, few traits or systems (character suites) can be argued to be constrained in any way. Indeed, over very long periods of time most functional systems are redesigned several times over, even to the extent that notions of

> homology, beyond the level of genetic and cellular processes, have little meaning. (Schwenk 1995, 259)[101]

Yet, Schwenk argues, and I agree, even when such selective pressures are operating, it is possible and indeed necessary to recognize non-selective developmental factors and the ways in which they sometimes restrict the range of phenotypic variation upon which selection can act. (Schwenk 1995, 255) (Maynard Smith et al. also agree on this point, they argue, however, that such cases are infrequent and, in any case, very tough to distinguish from the action of stabilizing selection. (1985, 281-2)) As such, a "maximally useful conception of evolutionary constraint must exclude natural selection as a causative (mechanistic) agent." (Schwenk 1995, 254)

Schwenk adds that not only is developmental constraint a "valid concept," it "is essential to any complete understanding of evolutionary patterns and processes" (Schwenk 1995, 251) That is, even though there a distinction to be made between the Class I patterns and the Class II processes, developmental processes and constraints are key factors, among others such as stabilizing selection, that shape macroevolutionary patterns. (Schwenk 1995, 251, 260-2) Schwenk diverges here from MS et al. in that he does not believe that such an approach will become bogged down in a causality quagmire since he argues that DC's can and must be studied as factors independent of selective pressures. For Schwenk, the independence of DC's is well established ontologically and poses no intractable problems from a practical research standpoint as the already

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[101] It is worth noting here that developmental systems may be redesigned at some stages while characters or the body plan remain. (Raff 1996, 224-7). Also Schwenk says "functional systems" and not morphological structures.

discussed case of Cerion's "jigsaw constraint" showed (CH2, VIII.2. Other well established cases were invoked by MS et al. (1985) and more recent studies will be discussed below.) And, as for the indented citation above, what may seem to be a contradiction is best understood as a qualification: even constraints that are eventually "broken" may have evolutionary significance.

V.2 Schwenk's Taxonomy: the Elimination of Historical and Universal Constraints

Schwenk makes at least two moves which distinguish his taxonomy of constraints from nearly all others. First, he dispenses with any notion of "historical" constraint. Whether one calls it contingency or "phyletic inertia" it is a condition which is true of all organisms at all times and, thus, "has little pragmatic value" (Schwenk 1995, 251) for those trying to apply the concept since, "Operationally, such a definition leads to the conclusion that all characteristics of all lineages are constrained during the entire course of their existence." (253) On this view, "constraint" simply means "evolved" and is therefore either confusing or redundant. (253)

Next to be eliminated is "universal constraint." Significantly, this category includes Gould and Lewontin's "architectural" constraint, Maynard Smith et al.'s physical and complex systems constraints (MS#1&2), and Resnik's "ahistorical." None of these nearly equivalent conceptions are useful for Schwenk since, he argues, they cannot account for lineage specificity. He states, "Such universal constraints certainly do set boundary conditions for the evolution of phenotypes, but they are ahistorical (in an evolutionary, if not a cosmic sense) and, therefore, are not a part of the universe of historical contingency." (Schwenk 1995, 253) In a strikingly novel move, Schwenk acknowledges their evolutionary significance—unlike neo-Darwinian Resnik (1995, 3) and some in evo-devo—*but he classifies them as a selective pressure*. Why? Because they are "a fundamental and unchanging part of the environmental milieu." (253) Furthermore, not only does he place physical forces such as gravity in this category, but also allometry. As such, he considers "many" structural, mechanical and functional constraints to be cases of stabilizing selection (253)! (See next section.)

One could argue here that because he recognizes the importance of such phenomena, Schwenk has at least one foot on the devo-evo side, despite the classification of the forces as "selective." Yet, this reclassification is both confusing and misleading insofar as such physical, structural, and complex constraint are not just part of the "environmental milieu" but the developmental milieu as well. That is, gravity is for larger organisms like us a universal physical factor external to organisms that restricts and makes possible various developmental and functional processes: they are neither lungs nor respiration without gravity. But calcium and calcification are requisite (internal) components in vertebrate development whose particular properties both constrain and make possible various developmental processes and structural features and functions. It is misleading to claim that the physical and chemical properties of (non-organic) developmental components are part of the "environmental milieu." And as I argued in the last two chapters, it is false to claim that such constraints are due the pressures of stabilizing selection (CH3, IV.1-IV.3; CH4, II.) or any mode of selection (Intro, III.2) Also, I shall return to the issue ahistorical and "universal" constraints later in this chapter.

In sum, Schwenk's taxonomy, and his conception of *selection*, breaks with his predecessors on several counts. The main reason for this, he says, is that he wants to drastically narrow the conception of DC's in order to make it more operationally useful. The elimination of the categories "historical" and "universal" combined with the reclassification of physico-chemical and complex systems constraints facilitates such a project. However, as I argued above, even if there are good (operational) reasons for eliminating such factors from the category of DC's, it is by no means clear that they should fall under the category of stabilizing selection. Yet, Schwenk's elimination of the possibility that any mode of selection is ever a cause of DC's emphasizes, I believe, that further research into non-selective aspects of development is both critical and practically feasible (contra MS et al).

But, Schwenk does criticize process structuralists as well. He argues that morphological stasis is not be regarded as prima facie evidence of DC's, hence the hard and fast distinction between Class I and Class II constraints. (Schwenk 1995, 251). Thus we can and should speak of constraints in morphospace without making assumptions about their causation. For example, body plans indeed persist, but they are not to be regarded as automatic evidence of some kind of developmental constraint. Schwenk allows that selection may play a role in the production of these and other evolutionary patterns. Generally speaking, process structuralists deny such a macroevolutionary role for selection, though Gould's view is more complicated.[102] Resnik also argues for a variation of this point when he makes the distinction between pattern and constraint: not

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[102] Species selection might play such a role as Gould argues (Gould 2002). But neo-Darwinians and most adaptationists do not recognize such higher level selection so this option is not available to them. I will not take a position on species selection in this dissertation.

all developmental patterns constitute constraints on adaptation. (Resnik (1995, 1-3) This is, in turn, a derivation from Amundson's distinction between constraints on form and constraints on adaptation. (Amundson 1994) However, while Resnik sides with neo-Darwinism, *Schwenk does not offer any evidence of the view that selection is a significant factor in the production of Class I constraints, nor does he urge it as a major one to pursue*. In particular, he offers no answers to criticisms that extrapolationist microevolutionary selectionist accounts have faced (Arthur 1997, 81-100) Indeed, as we shall see in the next section, the persistence of what Schwenk and Wagner call "evolutionary stable configurations" (ESC's) provides yet another reason to believe that selectionist accounts are not able to explain the persistence of major aspects of body plans.

The final point of this section leads to the next section. It is important to recognize that conceptions of selection are being articulated that no longer adhere to the hard and fast distinction between the internal (developmental processes) and the external (selective pressures).[103] A further articulation of this transgression between previous

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[103] That is, adaptationists traditionally approach morphology from the standpoint of immediate selective pressures—and, when pressed, past selective pressures. Developmentalists explained morphology in terms of developmental processes and structural demands that can be understood independent of the adaptive value of such traits. Recognition of the contemporary persistence of this impasse between the forms of explanation employed by adaptationists and developmentalists was expertly shown by Amundson (1994). Evo-devo is, of course, a significant recent contributor that has aided in demonstrating the limitations of externalist adaptationism. Those arguments are common enough that I need not replay them here. (Gould and Lewontin 1979, Raff 1996, Arthur 1997). However, an examination of the developmental side often reveals so-called "internalist" tendencies. In general, when one adopts the model that "development produces biased/variant phenotypes" and selection "sorts and/or eliminates" among those variants, internalism and externalism--symmetrically one might say--both persist (rightly or wrongly). Again, this two-stage conception of evolution can

forms of developmental internalism and adaptationist externalism can be found in the concepts of internal selection, coadaptation, and Evolutionarily Stable Configuration. I will argue that this triad of concepts undermines the distinction between evo-devo and devo-evo and changes the scope and context of the DC's debate.

VI.1 The Debate Shifts: Constraints, Internal Selection, Coadaptation and ESCs

A Quick Recap

Gould and Lewontin and Alberch had three major criticisms of the Adaptationist Program: 1) its conception of trait is "atomistic" and ignores or misunderstands the integratedness of the organismic architecture; 2) it overestimates the power of selection as an optimizing agent; 3) it fails to conceptualize and investigate other developmental and structural factors that shape the morphology of organisms and it cannot explain macroevolutionary patterns of change and persistence. Since the rise of evo-devo, these accusations against the Adaptationist Program are not as appropriate. Within evo-devo, there are adaptationists who acknowledge the integratedness of the organism as exemplified by one or more of the following: the persistence of developmental constraints and phylotypic stages, the correlation of characters, and the widespread existence of homologous and "standard" parts, and/or body plans. Indeed, it is part of the mission of evo-devo to explain such persistences and patterns of change. The point is that adaptationism itself has evolved. This "evolution" goes far beyond Dennett's reformist "reverse engineering perspective" which considers attention to mechanical and

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be seen in the work of early developmentalists such as Alberch 1980, 1982a, 1982b) and Goodwin (1994, also see Amundson 1994).

structural features to be a necessary part of AP because the evo-devo AP offers its own accounts of developmental integration. Dennett did not consider this to be necessary. (See my Ch2.) This marks a decisive switch in positions. It is used to be that the existence of developmental integration showed a weakness of neo-Darwinism's externalist AP and its tendency to atomize traits. Relatedly, in Amundson's language, the AP failed to realize that "constraints on form" will sometimes limit the range of adaptive possibilities given a specific regime of selective pressures—that is, constraintsF that led to constraintsA. The recognition of such "passive" constraints drove much of Gould and Lewontin's criticisms of the AP and its faith in the power of selection. But Arthur (1997) has changed the terrain in which this debate is waged.

VI.2 Arthur's Selectionist Evo-devo

In his *The Origin of Animal Body Plans* (1997), Arthur recalls and develops a concept from the forgotten work of Lancelot Law Whyte (1965) in order to overcome the externalism of the AP. Whyte, sounding like a contemporary devotee of evo-devo, argued, "The statistical theory of populations must be complimented by a structural theory of individual ontogenesis and of its influence on ontogeny." (Whyte 1965, 32) His own structuralism was developmentally inclined and led him to postulate two interrelated concepts—"internal selection" and "coordinative conditions"--to explain the integration seen among the developmental processes comprising an organism. I shall now discuss them in their contemporary form and explain how they bear upon the debate over developmental constraints especially in regard to their relationship to selection and adaptation.

Arthur argues that there are two forms of adaptation: "external" and "internal." Though the terminology may be novel, the distinction is not. For example, in the classic case of the tetrapod limb it is evident that its modification and divergence into "avian wings, mammalian legs, pinniped fins and so on is caused by selection for adaptation to particular environments and to ways of moving about within them." (Arthur 1997, 148) Yet, the persistence of the basic limb plan, "the retention of certain bone/joint arrangements--such as the articulation between humerus and radius/ulna despite adaptive divergence is caused by the need for *internal* coadaptation [my emphasis]." (148) That is, some features operating within a developmental context are preserved because of the contribution they make to the stability of the "local" ontogenetic mechanism (e. g. a limb field) or the developing organism overall. Furthermore, some features are even modified to increase their contribution to local or overall stability independent of their contribution to the organism's dealings with external selective pressures. Many homologies and developmental patterns are good candidates for such *internal coadaptations*. Thus, for Arthur, there are TWO selective milieu's, the internal-developmental and the external-environmental one. (From here on, I shall distinguish between the two as internal selection (IS) and external selection (ES). Both, it would seem, contribute to fitness in the classic sense: reproductive success. But, the same feature may have different or even conflicting adaptive values, as well as "roles," depending on the milieu considered: i.e. it may contribute to internal adaptation but interfere with external adaptation or vice-versa.

On this internalist (co)adaptationist view, developmentalism and adaptationism seem to meld together as a formerly externalist concept is applied to the internal developmental milieu. Interestingly, however, Arthur's conception differs from the ways in which Maynard Smith et al. and Schwenk (1995) introduced and applied the concept of selection to developmental, and developmentalist, terrain. Internal coadaptation need not result from stabilizing selection. Arthur argues that "there is not a general correspondence between external/directional and internal/stabilizing [selection]—rather all four combinations are possible." (Arthur 1997, 148) For example, stabilizing selection may occur on a developmental process in order to avoid variation in some adult morphological feature because of its high adaptive value and/or because any alteration in the feature decreases its adaptive value—i. e. it's on a peak in an adaptive landscape. As discussed before, there is much debate on whether what appear to be developmental constraints are actually stases enforced via selective pressures.

Stabilizing selection eliminates or wards off variation because of the (external) adaptive value of some feature, but Internal Selection (IS) is of a different order. Arthur argues that there is also selection upon genes not because of their contribution to the traditional adaptive value of some trait but because of the way in which they interact with other genes in the developmental milieu. (Arthur 1997, 148). "Internal selection" functions to increase the adaptive value of an element in the ontogenetic system relative to the demands of the organism as an integrated developmental system.

The work of Schwenk and Wagner (Schwenk 2001, Schwenk and Wagner 2001 and Wagner and Schwenk 2000), has shown how the concepts of internal selection and coadaptation can be applied in research on functional morphology and its evolution. Part of the power of their approach is that they have conjoined two recent developments in evo-devo—the concepts of internal selection and coadaptation and recent work on modules. Their program is to seek out and explain what they call Evolutionarily Stable

Configurations (ESCs). What Schwenk and Wagner do is take Arthur's notion of coadaptation and narrow its scope of application.

Schwenk and Wagner agree with Gould and Lewontin and Arthur that there is integration among characters and such integration is why externalist adaptationist programs are likely to misunderstand the way in which selection operates and what it works on. However, their focus is not on the *developmental* integration of processes or characters but on their *functional* integration. (Schwenk 2001, 174) Though this might lead some to claim that they no longer are within the provinces of evo-devo or devo-evo, I will argue that both their work and their conclusions are important for the debates discussed thus far in this dissertation. This is the case because of the interface they construct among function, morphology and development and the implications for explaining evolutionary patterns of stasis and change pursued by the morphospace studies discussed above and in general the relationship between process and pattern (as in Schwenk's distinction between Class I and Class II constraints).

VI.3 ESCs: The Case of the Lingual Feeding Mechanism in Squamate Reptiles

Schwenk and Wagner articulate their conception of Evolutionarily Stable Configuration with great detail in regard to a case involving the prey-capturing mechanisms in squamates (lizards, snakes, amphisbaenians. (Schwenk 2001, 186)). This case fits well within the mission of this dissertation since such mechanisms involve major features from both morphological and developmental perspectives: the adaptive importance of feeding mechanisms is as obvious as it gets, and in vertebrates, feeding involves many different processes, parts, and mechanisms so the assembly of structures involved constitute major elements of the vertebrate body plan (e. g. head, jaw) and involve major developmental processes (e. g. neurulation).[104] In this case, there are five distinct functional stages: subjugation, ingestion, processing, intra-oral transport, and swallowing. The internal selection on all the morphological components involved is likely to be strong because each is necessary for the carrying out of the function. (Schwenk and Wagner 2001, 555)

Many lizards apprehend their food items using their tongue. This "lingual ingestion" mechanism constitutes an ESC because it has a "proper function" in the classic evolutionary sense defined by Millikan: "the proper function of a system refers to its historically based, adaptive "purpose", essentially the architectural *raison d'être* of the system."[105] (cited in Schwenk 2001, 187) The proper function of the lingual prey mechanism is "prehension of small food items with tongue." (Schwenk and Wagner 2001, 555) Such a functional unit has many components including elements of the head and jaw, and, the star of the show, the hyobranchial (tongue/throat) apparatus itself with its adhesive mechanism. Indeed, without an effective adhesive mechanism--which involves a combination of "frictional interlocking and glue-like mucus"—the system cannot perform its proper function. (Schwenk 2001, 188)

Although lizards of the clade Iguania "evince nearly every diet, habitat preference, and ecological specialization possible for a lizard," the lingual prey

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[104] "Individual characters might participate in more than one functional unit, but a functional unit is uniquely characterized by a set of characters that all function together to perform a particular biological role." (Schwenk 2001, 172)

[105] I quote Schwenk here because the use of the modifier "architectural" indicates a split with the *Bauplan* perspective of process structuralists. That is, a structural element's "purpose" is to play a "proper" functional role, not a nonadaptive structural one. We will return to this key split below.

mechanism is remarkably uniform throughout the clade. (Schwenk 2001, 188) Schwenk argues that there are, therefore, no particular external (environmental) conditions that could account for the persistence—and lack of variation--of the mechanism. That is, an adaptationist would expect that differing niche conditions/selective pressures would lead to the modification of the key feature under consideration. Traditional adaptationist explanations do not explain the persistence of the configuration of features in this case even though its "adaptive value" is unquestionable!

To make matters worse for the adaptationist, there is evidence that there are strong (external) selective pressures to modify the foretongue so as to improve its ability for (vomeronasal) chemoreception (ability to detect various chemical aspects of the environment, especially those involving prey trails and the presence and sex of conspecifics and competitors). This is evident because, though tightly integrated, the functional constraint on the lingual prey mechanism has been broken, once in the *Scleroglossa* clade that evolved *jaw* prehension. (Schwenk 2001, 188) This "freed up" the tongue for the evolution of chemoreception since the adhesive mechanism was no longer necessary for the previous proper function of feeding (found in the common ancestor) and selective pressures were intense and consistent. The emergence of this novel feature is not associated with any ecological change or specialization, dietary or otherwise. (Wagner and Schwenk 2000, 165)[106] Thus, the constraint was not broken because of a change in selection pressures.

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[106] For more on how and why the functional integration was broken, see Schwenk and Wagner (2000), 181-9.

Although all Iguania have the ability for some tongue chemoreception, those with the lingual-prey mechanism are severely limited in this capacity (thus they rely more on their visual sense). But vomeronasal chemoreception requires a narrower and thinner foretongue that can flick. All these and other associated features directly impede the throat/tongue apparatus' ability to capture prey. Thus, "foretongue optimization for lingual feeding is in *direct conflict* with optimization for chemoreception." (Wagner and Schwenk 2000, 172) This conflict results from the opposition of internal and external selection. Internal selection is defined by Wagner and Schwenk (2000), building upon Arthur (1997), as rank-invariance of fitness across a range of environments and rank-dependence of fitness on the particular combination of traits possessed.

VII. Conclusion: Internal Selection, ESCs, and Developmental Constraints

Schwenk's Evolutionarily Stable Configurations are likely to be major components of *Bauplane*, (Schwenk 2001, 195) insofar as they are functions which often involve major structural features and this functional integration of features often persists over macroevolutionary time; that is, there is not much modification of the elements of the ESC since such change may interfere with proper functioning. As such, ESCs may constitute major macroevolutionary patterns as articulated by Schwenk (1995) in his description of Class I constraints and in morphospace studies favored by Raff and Arthur. But what is also of importance is how the notions of internal selection, coadaptation, and ESC come to bear upon earlier discussions of developmental constraints and Hall's evo-devo/devo-evo split.

The concept of ESC constitutes an important criticism of neo-Darwinism and standard adaptationism but it stops short of a devo-evo or existing process structuralism. The reason is that even though ESCs cannot be explained by external adaptation, they are not directly linked to developmental constraints whether "active" or "passive." (Gould 1989a, Resnik 1995) Schwenk claims that their stability and persistence is "emergent" and not due to some gene sequence or developmental mechanism alone because different kinds of characters involved in the construction of an ESC are produced by a mix of factors (e.g. neurulation, morphogenesis, etc.). These factors include but are not limited to "ahistorical" mechanical and structural constraints.[107] (Schwenk 2001, 182-3, 189) However, the more embedded the ESC, as in the case of Iguania, the more likely its persistence is due to all three major factors: developmental constraints, functional constraints (internal selection), and external selection. (190)

Recent case studies of developmental constraints have reflected this narrower approach to the topic as can be seen in Arthur and Farrow's (1999) study of centipede segment number and Gilchrist et al.'s (2000) study of wing shape in *Drosophila*. In both cases, the importance of a DC is demonstrated, but its connection to the overall configuration of the body plan is not. As I have been arguing, process structuralism's organocentric proclivities often drive it to suppose that developmental constraints are responsible for an organism's overall morphological layout as in Gould's earlier study of *Cerion* (1989) which leans in the direction of Gould and Lewontin's *Bauplan* Paradigm. But more recent studies such as Arthur and Farrow (1999) are narrower in their focus and make claims only about particular features, not body plans as such. For example, Arthur

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[107] But even if all the components were due to particular DC's, the functional ordering of the components is not bound to the temporal production of components and DC's result

and Farrow demonstrate that in geophilomorph centipedes, quite curiously, while there is incredible variation in segment number (from 29-191), there are no species (out of 1000) which possess an even number of segments. An ontogenetic mechanism seems to be the cause for this unlikely morphological distribution. (Arthur and Farrow 1999, 189) Here the focus is on the variation of one kind of segment, not some Centipede *Bauplan*.

A possible negative implication of the ESC concept for the process structuralist notion of *Bauplan* is that ESC may limit the possible importance of developmental factors by explaining major morphological persistences in terms of function rather than development and structure. The novelty of the ESC approach is that it does not invoke traditional forms of selection to do this. Thus, the triad of concepts of internal selection, coadaptation, and ESC stand as alternatives to both strongly developmentalist process structuralism and adaptationism in general, including the strain of adaptationism that explains developmental constraints in terms of stabilizing selection. This triad of concepts also marks a departure from the debate over the significance of developmental constraints by forwarding an internalist approach which is not development-centric but recognizes the shifting interplay of functional, development, and selective factors. Such an approach is process structuralist yet pluralist, just like my POPS approach. Yet, this view preserves a space for the exploration of developmental constraints as an important project for all those interested in an evolutionary developmental biology in the broadest sense and morphological macroevolution in particular. And, although it does not endorse the strongly internalist devo-evo view that developmental systems direct evolution (no one really does), it does emphasize that characters must be understood as developmental,

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from the latter. (Schwenk 2001, 182-3, 189) functional, and structural intra-organismic associations, and these are the diverse systemic conditions with which selection must work.

CHAPTER SIX:

PART TWO OF THE CONCLUSION: MY TAXONOMY OF CONSTRAINTS AND PROCESS STRUCTURALIST APPROACH

I.1 Intro to the Conclusion: a personal and polemical note

Two of the outside readers who read earlier versions or sections of this dissertation remarked to me that I took Gould and Lewontin's (1979) too seriously. That infamous article, they said, was styled more as a incendiary polemic than prolegomena to some future (process) structuralism. Knowing Gould's other works, I disagreed, especially after reading the essay (Gould 1989a) on the "jig-saw constraint" in *Cerion.* But the criticisms leveled by Dennett (CH2) and others struck a chord: it seemed true that Gould would occasionally propose some provocative and anti-orthodox (i. e. anti-neo-Darwinian) concept or argument and then either back off in regard to its radicality and significance or he would fail to *develop* the argument. This is, I would admit, perhaps most true of the notion of the *Bauplan* though less true of Gould's structuralism. It was part of the mission of this dissertation to pursue and develop these notions so provocatively tossed into the fray by Gould and Lewontin because I thought there really was a view ready to be unfolded. This potential view had not been properly developed in full by other sympathetic commentators, and its viability and desirability was ignored in the mainstream debates. But then "it" happened. What every dissertation candidate fears most materialized, and in monstrous proportions. Its name is *The Structure of Evolutionary Theory.* Its author is Stephen Jay Gould. Its length is one thousand four hundred and thirty-three pages. As it turns out, only FIVE HUNDRED or so of the pages bear upon the issues of structuralism and constraints. How fortunate for me that one of the main figures of my dissertation decided to release his masterwork a few months before I'm to defend and in it he has--to the surprise of so many--developed the structuralist views found in his infamous earlier essay with Lewontin and articulated and contextualized so many of his most provocative concepts and positions within this framework! Gould himself, after all these years, has finally spelled out, and in great detail, the history, nature, and structure of his structuralism and its pivotal role in his view of "this view of life."

I offer this story as both vindication and caveat. Gould's (2002) demonstrates the absolute centrality of the themes of development, morphology and constraint to his view of evolution--which is decidedly not just a matter of punctuated equilibrium and species selection. It also demonstrates that the "Spandrels of San Marco [...]" contained the real seeds of this view, as he himself notes (2002, 1249). However, it is not the mission of this dissertation to explicitly confirm or dwell upon the continuity between (1979) and (2002). What I aim to do is draw upon specific elements of Gould's (2002) which directly bear upon the nature and significance of developmental constraints and the evo-devo/devo-evo divide. Most relevant is his much more extensively developed concept of "spandrel" and its connection to the notion of exaptation and evolvability. I am NOT representing or evaluating Gould's view *in toto* as it's laid out in his (2002). Also, it is worth noting that Gould does not adequately evaluate all the issues and figures in the DC's debate though his view certainly bears upon and contributes to it. It is of course a tragedy that he will not be around to participate in the debates surrounding what I believe will end up being considered one of the great works in post-Modern Synthesis evolutionary biology.

I.2 Mission and Structure of the Chapter

This concluding chapter lays out the following: a criticism of selectionist attempts to explain developmental integration, my own taxonomy of constraints and its virtues, the "constraints" paradox for developmentalists resulting from Gould's notion of "cross-level spandrels," and the final details of my outline of a pluralist organismic process structuralist, or "POPS," approach to development and evolutionary morphology. The chapter proceeds as follows: the Functionalist Challenge from Evo-devo: ESC's and the limits of Internal and External Selection; My Taxonomy of Constraints; On the Special Status of Active Constraints: Gould's "Cross-level spandrels" and Newman and Muller's theory of Epigenesis; My Process Structuralism.

II.1 A Functionalist Challenge from Evo-devo: ESC's and the limits of internal and external selection

As explained in the last chapter, internal selection is a concept created and deployed by recent developmentalist adaptationists (i.e. practitioners of evo-devo) to explain the phenomena of developmental integration. Internal selection is an "adaptationist" concept insofar as it explains the aspects of a "trait" relative to the fitness contribution it makes to the organism given the demands set by a particular milieu. In this case the milieu is not the traditional 'niche" (external environment) but the developing organism itself (Wagner and Schwenk 2000, 157-60). In such cases, "fitness" refers to the reproductive advantage that comes from the increased ontogenetic stability. Ontogenetic stability or "homeostasis" as Alberch called it, is partially a result of the structural, developmental, and biochemical interconnectedness of different developmental mechanisms.

Internal selection (IS) is not just another mode of selection ala directional, optimizing, or stabilizing selection, nor is it just another unit or level of selection ala group selection, individual selection, or gene selection. The reason for its special status is that all those other modes or levels of selection are within the traditional framework of the externalist AP, i.e. the contribution of a trait to the reproductive success of an organism or group etc., relative to the demands of some external environment. IS changes, and broadens, the notion of what counts as an "environment." This point is effectively captured in Wagner and Schwenk's definition of IS as rank-invariance of fitness across a range of environments and rank-dependence of fitness on the particular combination of traits possessed. (CH5, IV.)

I consider the acknowledgement of "internal selection" by evo-devo to be a major victory for process structuralism. The notion that the primary purpose of certain morphological features—whether embryological or adult--is to contribute to the developmental dynamic's stability or efficiency constitutes a significant shift for the AP. While the notion of functional trade-offs has been at least theorized by adaptationists for more than two decades (see Dawkins (1982) for one noteworthy example), though seemingly organismic, such a notion actually reinforces the idea that an organism is not integrated but just a jumbled set of discrete parts. The notion of internal selection pushes the AP even further into devo-evo territory. As was discussed last chapter, this is true because IS involves the idea that features may be modified for purely developmental reasons—indeed, IS could even be called “developmental” selection!--and these developmental factors are independent of traditional (external) selective pressures sought after by the AP.

A further consequence of the IS concept is it fosters a more organismic approach as is often favored by structuralists and non-genocentric adaptationists. As Gould and Lewontin and many others have noted, Darwin too had a organismic focus and considered the role of embryology in evolutionary theory to be crucial (Hinchliffe 1994, 163). However, since the rise of the Modern Synthesis, the atomizing tendencies of the AP have often inappropriately undermined such an organismic approach as genetic and molecular reductionisms have literally dismantled the organism as both an integrated developmental, functional, and structure system, and as an evolutionary actor. As I have argued throughout this dissertation, this has caused the AP to suffer from many explanatory inadequacies such as its misidentification of traits and the inability to explain and even recognize persistent macroevolutionary patterns such as phylotypic stages, body plans and evolutionarily stable configurations (ESCs). In sum, the concept of internal selection brings a developmentalist and organismic approach to the AP. This constitutes a significant change since the externalist approach to trait modification must now not only take into account possible developmental constraints, but that the reason for the existence of certain aspects of a trait will sometimes be due to the contribution it makes to the developmental stability of the organism. This is especially likely to be the case with what have long been called “homologous” features. Not only will many features that have eluded previous adaptationist accounts be good candidates for IS, but morphological *aspects* of characters that make significant contributions to traditional fitness may actually be the result of IS.

II.2 Selectionist Explanations Cannot Explain the Range of Available Variation

Although internal selection is a concept deployed by adaptationists, it is thoroughly developmentalist and thus can be used by process structuralists as well. However, as is the case with all key concepts, its scope of application must be carefully delineated. Thus, although IS makes a critical contribution to the evo-devo AP and devo-evo, it has also shifted attention away from a critical issue: the range in which trait modification takes place.

Internal Selection is not sufficient to explain developmental integration, nor does it explain the generation of particular morphologies. While IS pushes us to recognize that the primary benefit of some trait change or gene selection might be developmental rather than "functional," it does not explain what determines the viable range of modification. In other words, internal selection, like all modes or levels of selection, requires that there be intraspecific variation in the population. But, it does not explain the range of that variation, (assuming there is variation). Selection in any guise requires intraspecific heritable variation. But what drives the developmental constraints debate is how to explain the *range* of variation and persistent long-term evolutionary and developmental *patterns*. Internal selection begs the question and thus can play only a limited role in the explanation of the developmental integration of organisms and evolutionary morphology.

For example, in regard to the already cited case of the tetrapod limb, Schwenk (2002) surmises that the "failure of terrestrial vertebrates to evolve more than five digits is probably the result of harmful pleiotropic effects of [genetic] mutations that increase digit number." (5) Polydactyly appears sporadically in mutants, but deleterious side-effects probably outweigh the benefits of the extra digits. (Schwenk 2002, 5) That is, the restriction on variation is due to the demands for internal coadaptation. But this explanation raises a number of problems.

It appears that Schwenk is assuming, like many others, that digit number is under the control of particular gene sequences. This view is called the 5-domains 5-digits view. But this view, and variations of it (see Raff 1996, 347-51), has also come under an array of criticisms for a number of reasons. First, there is evidence that undermines the claim that there are five discrete domains. (Hinchliffe 1994, 167) Second, there are continuing controversies over the relationships among many of the different agents –the AER, ZPA, Hox genes, mesenchyme. (Gilbert 1999, 725-7) But if we acknowledge the basic precept that development is "hierarchical" (see my Intro, III.)—as does contemporary developmental biology, evo-devo and devo-evo—then it is not possible that there is one causal actor that directs the show. Hinchliffe warns that a "consequence of the domination of analysis of limb development by single factor one-step mechanisms (whether [genetic]domains or ZPA) is the diversion of attention from experiments demonstrating sequential local interactions, including epithelial/mesenchymal ones." (Hinchliffe 1994, 167) For example, termination of the activity associated with the apical ectodermal ridge (AER) will reduce the digit number. And a shortage of mesenchymal cells—for whatever reason---leads to the loss of the elements formed last (the digits) whatever the adaptive value of these distal parts. (165)

Though there is some variability in digit number and supernumerary digits are easy to add experimentally (via ZPA grafts, not genetic modification) the rest of the limb (radius and ulna and other phalanges) is conserved both developmentally and morphologically. That is, *the (temporal) position of each in the production sequence does not vary nor does its relative spatial position in the fully formed limb of the adult.* Hinchliffe, following Alberch (1989), argues that this process of limb morphogenesis is operating under a developmental constraint. I agree with this assessment but it also needs to be noted that, following Alberch, while this persistent pattern is a constraint on form it has not been clearly demonstrated that it is a constraint on adaptation.

Although the invariant aspects (radius/ulna, tarsals) are clearly a DC, the variable elements (e.g. digits) are also operating under a constraintF. That is, even though these elements are modified in quite diverse ways to support and enact flying in bats, digging in moles, and swimming in dolphins, it is still likely that the DC is present because of the dependence of digit formation on the structures and processes that immediately proceed it. Again, although there is variation here, it happens within a restricted range: there have never been more than 7 or 8 digits, and the middle digit is always the longest. In sum,

> this structural outcome is related to relatively minor changes in limb bud boundaries arising through alteration in mesenchyme cell number or in the period of AER activity. Quantitative changes in cell number would readily result in distal qualitative changes e.g. in digit number. Such distal channeling of structural change may represent a developmental constraint very similar to that proposed by Alberch. (Hinchliffe 1994, 165)

III.1 My Pluralist Organismic Process Structuralist Taxonomy of Constraints ("POPS"); Process and Pattern; Pluralism

The distinction between constraints as patterns and constraints as processes is one that I accept. The assumption that macroevolutionary patterns necessarily are evidence of developmental and structural constraints assumes too much. But the assumption that such patterns must be due to selection and therefore constitute adaptationist landscapes also is unwarranted. Disproving the latter was part of the mission of Alberch whose morphospace studies and concept of constraint do not deny selection, but indicate at the very last that what is selected for and how the system responds "do not necessarily map onto each other very closely." (Raff 1996, 299)

Contra Maynard Smith et al., attempts to classify all constraints as "developmental" leads to obfuscation. There are certain aspects of organismic morphology, from components in development to adult body plans that transgress the category developmental and head into the structural and/or functional. For example, Schwenk's notion of the ESC stands as a (functional) constraint from the perspective of selection. But it is also a constraint on adaptation and a constraint on morphology and thus within the purview of this dissertation. Yet according to Schwenk, it could not be classified as "developmental" since its persistence is not due to the dynamics of some ontogenetic mechanism. As I have argued since Chapter Two, one of the virtues of process structuralism is that it has pursued a program which consistently takes into account structural, functional, and developmental factors, especially in regard to selection. And Schwenk and Wagner's ESC concept can benefit process structuralism as well since ESCs are another mode of stasis/constraint and may involve major elements of a body plan. Development-centered views like MS et al. tend to downplay or even ignore the structuralist concerns, though they ostensibly include them within their paradigm. That is, although there is an explicit agreement among adaptationists such as Dawkins, Dennett, and MS et al. that all these factors should be taken into account, adaptationism again and again fails to investigate their evolutionary role and significance.

My view takes an organismic approach consistent with most in devo-evo/process structuralism and a few in AP evo-devo (e.g. Wimsatt 2002) and offers a process structuralist account and taxonomy of constraints that is pluralist (POPS). On my POPS view, there are three kinds of constraints: structural, developmental, and functional. Such a taxonomy enables us to pay proper attention to selection, development, structure, and function without positing a pre-defined hierarchy among the four when it comes to the examination of a particular trait. Thus, there are "constraints" due to selection (stabilizing and internal selection), function (ESCs), development (a variety of DC's) and architectural or geometric constraints. And, there are some constraints which are also due to combinations of the preceding.

III.2 My Taxonomy of Constraints:

1. Developmental

1.1 due to demands of organismic homeostasis (CH3)

1.2 construction rules of particular developmental mechanisms, especially in morphogenetic mechanisms; (Intro, CH2-6)

1.3 canalization (diminution of variation possibly initiated by stabilizing selection but maintained ontogenetically) (CH3, 5, 6)

1.4 physico-chemical processes and materials (e.g. calcification, excitable media, adhesion) (Intro, CH2-6)

2. Formal

2.1 geometric and (some) architectural constraints (CH2, 6) (e.g. jig-saw constraint in *Cerion*)

2.2 physico-chemical processes that place demands upon the relational placement of features, especially in adult morphology (Intro, CH2-6) (e.g. Gould's "structural constraints" below)

3. Functional

3.1 ESCs (CH5-6)

3.2 physico-chemical processes (e.g. negative feedback loops, periodicities) (Intro, CH5-6)

4. Selectional

4.1 stabilizing selection (CH3-6)

4.2 "internal" selection (CH5-6)

Although I have discussed each subcategory at length in the chapters cited above, let me just add a few points. First, the reason I include selection on this list is for the following reasons. There is an important research project to be had in regard to ways in which selection impacts upon the internal dynamics of developing organisms since many of these affects were not recognized or sufficiently addressed by the externalist AP. Also, I would not want to rule out the possibility that selection and development act in conjunction in some instances to produce DC's. While, again, I contend that DC's independent of selection do arise and have evolutionary significance, there are going to be others resulting from combinations with selection and/or "structure." (More below.)

Second, in Chapter Two, I criticized Gould and Lewontin for their hard and fast distinction between "architectural" and developmental constraints. In many cases, architectural constraints are within ontogeny (e.g. Seilacher's shell formation processes). But in other cases such as the case of *Cerion*'s "jig-saw" constraint, the "formal" constraint is independent of the particular developmental mechanism employed and thus requires a separate category. As Gould put it in regard to *Cerion*'s jig-saw constraint, "this negative [formal] interaction expresses no biological principle (beyond the fact that snails coil); it merely reflects the three dimensional geometry of space." (Gould 1989a, 520). I believe that the name "formal" or "geometric" is better for the category than "architectural" because the latter could connote the inclusion of the building process which it should not. In any case, I do grant that there will be overlap between "development" and "formal" but they still require separate categories.

III.3 Assessing the Scope, Entrenchment, and Effect of Particular Constraints

Each of the kinds of constraints discussed above may be assessed or qualified via the following three criteria

1. Taxonomic Scope: local/universal (MS et al., Resnik)

-The Local/Universal distinction is effective and easy to apply. There are several studies that have identified taxon-specific DC's and patterns of change, from the quite local one of Arthur and Farrow's (1999) centipede to the subphyla-wide vertebrate limb. The evolutionary significance of such constraints is not necessarily lessened because of limited scope its (past or present) since, after all, that lineage may evolve many different subspecies (as in Beetles which all two million species share the same body plan). In addition, identifying a constraint in one lineage, even if short-lived or small in number, makes it easier to identify constraints in others.

2. Degree of bindingness or "breakability" (MS et al., Resnik): (see CH5, IV.1)

3. Effect of Constraint/What is Constrained?:

3A Is it a constraint on morphology and/or a constraint on adaptation? (Amundson)

3B What organismic aspect is constrained? (Schwenk)

-Developmental features and mechanisms (e.g. limb fields) including genetic architecture; adult characters; character complexes including ESCs; lineages; body plans. I do not regard this issue as settled. (Gould 2002, 1037n)

Throughout this dissertation I have principally focused on the constraining of the production of morphological variation in general, and most of the previously cited levels have been included.

4. Active/Passive: (see next section)

-**Active constraints** (Alberch, Gould (2002)): are "channels" for future variation and/or sources of evolutionary novelty and thus are less likely to be constraintsA (see next section)

-**Passive constraints** (Gould and Lewontin 1979, Gould 1989a, 2002, Alberch, Maynard Smith et al. 1985, Resnik 1995, Schwenk 1995): restrict the range of morphological variation such that they are constraints on form and more likely to be constraints on adaptation. (e.g. the DC's that inhibit the production of six-limbed vertebrates)

In general, as Schwenk (1995) urged, the operationalizing of terms is desirable and necessary. But the virtues of a taxonomy are not determined solely by its ease of application in the current research setting. A taxonomy inevitably draws upon or even constructs an ontology and epistemology and therefore must be linked to some "approach" or paradigm. The approach that informs my taxonomy is process structuralism as I have defined it throughout this dissertation. What can be operationalized are the subsets of particular categories, but, again, the construction and delineation of those categories requires a background ontology and epistemology and in this case an understanding of the concepts of organism, trait, and development.

IV.1 On the Special Status of Active Constraints: Gould's (2002) Cross-level Spandrels and Newman and Muller's Theory of Epigenesis

Though recognizing that "passive" DC's are sometimes evolutionarily significant is still more controversial than many admit--and intrinsically difficult for many adaptationists to accept--the real action is often said to center around the notion of active or positive DC's (Resnik 1995). Since I have repeatedly argued that the issue of the "range of variation" is absolutely central to the study of evolutionary morphology and so-called passive constraints are critical to this study, I am not in complete agreement with this take on the debate. But what is crucial about the active constraints debate is that it pushes our understanding of ontogeny in a different direction than the passive constraints debate. The difference is that from the start, the DC's debate has sought to demonstrate the ways in which ontogeny impedes the action of selection. On this view, development is treated as a hindrance to the production of optimal characters. (CH1&2) Even developmentalists encouraged this anti-adaptationist and anti-selectionist view. But the notion of "active constraints" treats development as a creative evolutionary force which channels variation and is a major source of evolutionary novelty. The following passage combines both views as it travels from the passive to the active conception.

> Developmental constraints are defined as biases on the production of variant phenotypes, or limitations to phenotypic variability, caused by the structure, architecture, functions, and dynamics of developmental systems. Such constraints are often viewed less as prohibitions than as *opportunities*, since they allow

> exploration of regions of genomic, morphological, or behavioral space in a nonrandom manner [my emphasis]. (Depew and Weber 1995, 481-2)

While the first sentence follows MS et al. and defines bias as "limitation," the second makes a break along the lines of Alberch, Newman and Muller and Gould and creatively redefines "bias" as "opportunity." Over the remaining sections, I will forward a two-tiered notion of this second "active" conception of DC's. The first draws upon Gould's recent work which has refined the notion of spandrels and placed it in the context of what he calls the "exaptive pool." The second involves Newman and Muller's theory of epigenesis which is very much at the core of my devo-evo/process structuralist view.

IV.2 The Return of the ("Cross-level") Spandrels

In Gould and Lewontin (1979), spandrel was defined a side-consequence of a design choice. (Gould and Lewontin 1979, CH2, III.2) Spandrel production is sometimes initiated by but never under the control of selection. This is because spandrels are not themselves responses to some selective regime but "byproducts" of responses to some selective regime. These indirect effects are due to architectural demands—or, as I pointed out (CH2, III.2), the variable interconnectedness of developmental processes. In his (2002), Gould dramatically refines and expands this definition of spandrel as an architectural constraint. But first we must locate the category within its proper theoretical approach before explaining its new subcategories.

For Gould, there are two kinds of structural constraints. The first are due to the properties of materials and physical laws and are consistent with earlier discussion in MS et al. and my own taxonomy above. [Gould 2002, 1053-4.) The second set of structural constraints are spandrels. There are two kinds of spandrels: "at level" spandrels arising because of geometry and "cross-level" spandrels which arise by "injection" from outside domains. The previously discussed pendentives of San Marco (CH2) are "at-level" because they are due to the geometry of the structure and the ordering of various sorts of elements. Interdependencies abound from the design perspective and pendentives arise in order to connect and support the dome on its four arches (in the case of St. Mark's). [Gould 2002, 1281-2.] A biological example of an at-level spandrel due to the "necessity of geometry" involves structures utilized for brooding by some land snails.

Many gastropods (one of the seven classes of molluscs) grow by coiling a tube around an axis. Such growth dictates that there be an open cylindrical space along the base of the axis. This space is called an *umbilicus*. The umbilicus is often narrow and filled with calcite—when this happens it's called a *columella*. But in other cases it remains "unfilled" and open, especially in land snails, and a few species use it as a brooding chamber in order to protect their eggs. (Gould 2002, 1259) The umbilicus, whether filled or unfilled, is a necessary byproduct of coiling; that is, it is a space arising due to a geometric constraint. That is, the property "coiling" was not selected for the function of "brooding." Indeed, that it is usually filled with calcite emphasizes this fact. (Gould 2002, 1259-60) As such, the open, unfilled space started off as a spandrel and then becomes an exaptation since it has an adaptive value but was not selected for.

Another case of a feature born of geometrical necessity involves the "Irish Elk" (*Megaloceros giganteus*). Many large herbivorous mammals also have large heads. In order to better support these heavy crania, muscles in the upper back and neck grow bigger and this leads to the elongation of the spine that supports them. All these changes are clearly adaptive—not having the support you need to keep your head raised and move is likely to cause problems and there appeared to be intraspecific variation available in the population. We shall also assume in this case, then, that this increase is due to selection. However, a side-consequence of this growth is not due to selection. The side-consequence is "bumps" upon the shoulders which arise because of the upward expression of the spine. Such bumps are geometrically inevitable but initially, undoubtedly, an at-level spandrel. However, after a period of time, these bumps became larger and gradually took on the size and shape of rudimentary antlers. At this point, the elongated spine goes from being a spandrel to an exaptation. That is, the side-consequence comes to have an adaptive value—antlers attract positive female attention and can be used against males whether as intimidating display or in actual combat. (Gould 2002, 1260.) It seems that this example would also be a "positive constraint" insofar these "bumps" open new opportunities for variation in regard to the size and shape variation of the new trait "antlers." (More below.) Once there is a selective regime in place and variation in the population which leads to fitness differentials among the members, the exaptation becomes an adaptation.

IV.3 Examples of Cross-level spandrels: Genetic Mutations, Beaks

When an organism is modified at one level over evolutionary time, that change may oftentimes affect elements or processes at other levels or in other systems. This happens among overtly interconnected systems—changes in the circulatory system which affect the respiratory system—and the not so overt: an alteration in eye formation which affects heart formation. (Raff 1996, 205) Some side-consequences will be lethal, others will lead to a decrease in fitness and the trait that caused the side-consequence may gradually be eliminated, if not the lineage. But many others will be "absorbed" by the developmental and morphological system. These side-consequences are non-adaptive and not under the control of selection either because of their neutrality and/or their invisibility to selection, or selection's present inability to modify them. Such effects are akin to genetic drift (genetic change that results not from the action of selection but from the dynamics of the developmental-molecular-genetic system). Non-adaptations that arise because of interactions at the same level or within the same system are again called at-"level spandrels." St. Mark's pendentives, the Elk's "bumps" and gastropod's umbilicus are examples of at-level spandrels. The key difference between the earlier essay with Lewontin and Gould (2002), is that cross-level spandrels are deemed to be of comparatively more evolutionary significance. (Gould 2002, 1288)

The most obvious example of a cross-level spandrel is a (genetic) point mutation. Such a mutation arises for a perfectly good chemical reason, not because of its effect on the upper levels of the organism (phenotype). Thus the phenotypic effect is "unintended," or, a side-consequence. (Gould 2002, 1268) Because genetic mutations affect non-genetic levels Gould calls them an "injection" to emphasize the cross-level aspect.

Another example of a cross-level spandrel involves Darwin's famous finches. Beak size and shape changes in response to changes in climate and competition with other species. (Podos 2001, Ryan 2001, Grants et al 1986, cited in Gould 2002, 1287) Such change in size and shape has "automatic consequences upon the form, style, and range of the resulting song, because "two functional systems—that used for feeding and that used for singing—share a common morphology, the beak (Podos 2001, 186)" (cited in Gould 2002, 1287). The difference is that sharper and narrower beaks enable both a wider auditory range and more precision for singing. The heavier and blunter beaks impede such range and precision. Podos correctly calls this morphological-functional correlation a "constraint." Songs are critical as a "pre-mating isolating mechanism" and for mate recognition so their adaptive importance is obvious. However, the changes in singing are not under the control of selection, rather, differential variation in song range is a cross-level (across functional systems in this case) side-consequence of selection on the same feature (beak morphology) for another function (feeding). (Gould 2002, 1287-8)

IV.4 Conclusion of Section

What Gould calls on us to recognize is that not only is evolution driven by selection working upon pools of available variation, it also is driven by a wide range of developmental changes that result in the emergence of features which are not responses to present selective regimes. While some are due to past selective pressures (e.g. vestigial traits), others are the result of developmental and architectural constraints, and still others are generated as side-effects of responses to a selective regime upon a particular trait. For Gould, this last set of non-adaptations have the most evolutionary significance for two reasons. One, Gould believes that their exaptive potential is greatest since "for intrinsic structural reasons, the number of potential spandrels greatly increases as organisms and their traits become more complex" (Gould 2002, 87). That is, complex systems when modified vary in numerous and unintended ways thereby providing a pool of variation to meet other selective regimes. Two, it finally explains the apparent paradox of what has been called the property of "evolvability." Selection eliminates variation so as to increase the relative fitness found in a population. But as it eliminates variation it indirectly spawns variation on other features and/or at other levels of the function/structural/developing organism. In other words, spandrels arise in spite of selection. Thus not only are they causally independent of selection in terms of their genesis, they actually make it possible by providing variants. For these reasons Gould goes so far as to state,

> Spandrels, and all other forms of exaptive potential, define the ground of evolvability, and play as important a role in macroevolutionary potential as conventional adaptation does for the immediacy of microevolutionary success. (Gould 2002, 87)

With the above theory of cross-level spandrels, Gould has identified another agent in the macroevolutionary process that is truly on par with selection. He has spelled out its causal details, and explained how it operates independently of selection in any mode—stabilizing, directional, internal, etc. Yet, with this argument for the centrality of cross-level spandrels as the pool of evolutionary potential from which selection draws, Gould departs from the view of Gould and Lewontin (1979). In that essay, they write, "Developmental constraints, a subcategory of phyletic restrictions, may hold the most powerful *rein* of all over possible evolutionary pathways [my emphasis]." (86) But, spandrels are very nearly the opposite of constraints, they are evolutionary novelties that mark the possible expansion of variation, not its restriction.

V. Are Cross-level Spandrels Channels for Variation? A Problem for Gould and Developmentalists

> When we move from simple tubes and sheets (aspects of universal geometry, even though evolved modes of growth in particular lineages must elicit the forms) to more complex developmental architectures that record the contingencies of particular lineages (rather than the general geometry of Euclidean space), both the range and the number of potential spandrels, and their capacity for future exaptive utility, must broaden enormously [...]. (Gould 2002, 1260-1)

In his (2002), Gould argues that passive or "negative" constraints are restrictions on variation and positive constraints are "channels" that enable more variation. These channels are set by the internal organization of the organism although natural selection may have to supply the "initial impetus," as was the case of the Irish Elk's proto-antlers. (Gould 2002, 1032) He adds that a "channel" arises when a group of items is forced "into closer conjunction so that their combined power and speed can grow and also become more focused in a particular direction towards a definite goal—as in the increased speed of fluid in narrow pipes, according to Bernoulli's principle." (2002, 1026) What puzzles, however, is the following: given the frequency with which spandrels are generated, especially among more complex organisms like vertebrates (see passage above), in what sense does an enormous exaptive pool constitute a channel? It almost seems to do the opposite; it is, after all, a *pool* not a canal. If exaptations were not generated very often and/or there was some sense that a process was circumscribing their production, then perhaps they could constitute a channel, or "canal." At-level spandrels might be more likely to channel future variation as in *Cerion*'s jig-saw constraint. Also, Gould's characterization of the case of the Irish Elk lends itself more readily to this kind of interpretation. The elongation of the spine and the emergence of the antlers seems to offer a channel for future adaptive possibilities of the Elk. I see this issue as unresolved, but given Gould's characterization, there are two options: either spandrels constitute an exaptive "canal" that makes available a particular flow of variation, or there is truly an exaptive pool but there is not much direction offered.

VI.1 Newman and Muller on Positive Constraints and Devo-evo

Newman and Muller also stress that development plays a pivotal creative role in evolution as the primary generator of morphological novelty. They argue that epigenetic mechanisms, and not genetic changes, are the primary source of morphological innovation. (2000, 305) As discussed in my Intro, they regard the most important epigenetic mechanisms to be

1) interactions of cell metabolism with the physicochemical environment within and external to the organism,
2) interactions with tissue masses with the physical environment on the basis of physical laws inherent to the condensed materials, and

> 3) interactions among tissues themselves, according to the evolving set of rules. (Newman and Muller 2000, 305-6; see 309-10 for examples: induction, etc.)

As we have seen, all of these epigenetic mechanisms are sources of novelty, and spandrels. But what they also point out is that these generators of novelty may channel the new variants:

> innovations initially originate as "pure" consequences of ubiquitous material and developmental propensities. Therefore generic processes can lead to similar forms in unrelated organismal lineages, manifested as the characteristic "homoplasies" of morphological evolution. (Newman and Muller 2000, 312)

Homoplasies are similar characters that arise in different lineages: i.e. the new characters are similar but not found in a common ancestor. For example, similar wing patterns have evolved independently in several different lineages of moths and butterflies because the developmental mechanisms of each abide by similar "construction rules." (Futuyma 1998, 110) Vertebrates and cephalopods, which are in different phyla, both independently evolved eyes. In this case, however, though there are similarities in the general morphology of these ocular structures, there are also significant structural-functional differences, and the developmental pathways which lead to the shared feature are different. When similar features arise in different lineages because of shared ontogenetic construction rules it is called "parallel evolution." When the developmental pathways are different it is called convergent evolution—and the resemblance then is considered more "superficial." Parallel evolution might seem to be a good candidate for a positive constraint since variation is generated yet the variation is channeled given the ontogenetic mechanisms operative and materials employed. However, in most cases of parallel evolution, there is a similarity in selective regimes as well. Yet, as was argued in my Intro, although animal ontogeny is notoriously complex, many of the components and processes that comprise it are fairly simple and in play throughout the various phyla of the kingdom. As Newman and Muller put it, much of animal morphology is largely a matter of

> molding clusters of dividing cells into physical shapes. Layers, sheaths, tubes, rods, spheres, etc. are formed by aggregates of cells, mobilizing a wide range of biomechanical forces that result from the different properties of different cell types and their extracellular products. (Newman and Muller 2000, 313)

Perhaps these basic and widespread ontogenetic mechanisms act as preliminary physico-chemical channels?

VI.2 Process Structuralism and Genocentrism

Even from a genocentric perspective, the existence of spandrels may be admitted. Futuyma sums up the argument in three sentences,

> When we speak of the function of a feature, we imply that there has been natural selection of organisms with the feature and *of* genes that program it, but *for* the

> feature itself. We suppose that the feature caused its bearers to have higher fitness. The feature, may, however, have other effects, or consequences, that were not its function, and for which there was no selection. (Futuyma 1998, 350)

But both Hall and Resnik claimed that a devo-evo would not be genocentric. Newman and Muller's process structuralism definitely meets this demand, "We propose that a synthetic, causal understanding of both development and evolution of morphology can be achieved by relinquishing a gene-centered view of these processes." (Newman and Muller 2000, 313) Their anti-genocentrism is coupled with their understanding of ontogeny as hierarchically organized nested set of processes. And key among these processes are physico-chemical processes that operate independent of selection.

For example, changing the stress placed on embryonic connective tissue and tendon insertions will generate novel sesamoids (e.g. the patella). In the avian hindlimb, four such movement-dependent sesamoids form during the course of normal development. However, as has been shown experimentally, if there is no movement, then there is no formation of these bones. This also has downstream effects since during later stages of ossification, these skeletal elements become incorporated into the longbones of the limb. This leads to novel limb shapes and limb bones because it alters the biomechanics of the embryo: "the resulting skeletal elements appear as novel characters of avian bones, such as the supratendinal bridge, the cnemial process, or the fibular crest of the tibotarsus" (Newman and Muller 2000, 312). All these are significant changes in bone morphology but none are due to genetic mutation or change for the character in question, “Rather they arise as side effects of mutations affecting other characters, such as the size or the growth rate of the tibia.” (Newman and Muller 2000, 312)

The explanation of the production of the novel characters in the above not only gives support for a non-genocentric developmentalism, it also is an example of an evolutionarily significant cross-level spandrel. This is true because the new characters result from changes upon the growth rate of a different character.

As for the issue of positive constraints (e.g. spandrels) and evolvability, for Newman and Muller, evolvability “represents the continued efficacy of epigenetic processes in a lineage.” (2000, 306) In fact, they argue, the primary role of genes is to *reduce* phenotypic variability in order to preserve the traits with the greatest relative fitness:

> genetic change is required for evolution to progress, but with respect to morphology, it mainly plays a consolidating role, rather than an innovating one. Physically determined morphogenesis becomes secondarily captured and routinized by genetic circuitry that thus serves to channel and reinforce epigenetic propensities. (Newman and Muller 2000, 315).

From this perspective, selection “functions to release and consolidate inherent developmental potential, rather than guiding morphological evolution directly.” (Newman and Mulller 2000, 314) That is, genetic change and selection often generate morphological side-consequences which arise due to the properties of materials and the propensities of developmental mechanisms. After this variation is generated, selection then acts to "consolidate" or eliminate variation. But again, because complex systems respond in novel ways to (selective) modification, novel features in most lineages continue to be generated. But the range of this variation is framed by the developmental systems even if frequently eliminated. Returning to my own taxonomy, if this range of variation enables much future variation it is a positive constraint, if it restricts it, then it is a negative constraint.

Furthermore, this concluding case not only brings together Gould and Newman and Muller on the theme of negative and positive constraints, it also demonstrates the virtues of a process structuralist view that is organismic and internalist and recognizes the multidimensional interconnectedness of the organism as a hierarchically organized nested set of developmental, functional, and structural systems and the significant creative and regulative roles of these systems in the generation and modification of evolutionary morphology.

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