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DARWINISM, PROCESS STRUCTURALISM, AND NATURAL KINDS

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Darwinists classify biological traits either by their ancestry (homology) or by their adaptive role. Only the latter can provide traditional natural kinds, but only the former is practicable. Process structuralists exploit this embarrassment to argue for non-Darwinian classifications in terms of underlying developmental mechanisms. This new taxonomy will also explain phylogenetic inertia and developmental constraint. I argue that Darwinian homologies are natural kinds despite having historical essences and being spatio-temporally restricted. Furthermore, process structuralist explanations of biological form require an unwarranted assumption about the space of developmental possibility.

1. Phylogenetic Inertia. There is widespread, if often tacit, acceptance of the existence of 'phylogenetic inertia'. Lineages continue in their adapted state when the selective pressure responsible for that state is removed. The idea is taken to an extreme in Stephen J. Gould and Elizabeth Vrba's (1982) concept of 'exaptation'. A trait is an exaptation for some function if it now serves that function, but its initial spread in the population was not caused by its serving that function. If feathers were originally selected for their insulation value, then they are an exaptation for flight. Gould and Vrba suggest that it is inappropriate to offer adaptive explanations of exapted traits in terms of the functions they now perform, or any functions they may have performed subsequent to their initial spread in the population. It is even inappropriate to regard these later, fitness-enhancing effects as biological proper functions of the traits in question.

An assumption of phylogenetic inertia also underlies the conventional view in comparative biology that several taxa which inherit a trait from a common ancestor count as one example of that trait rather than several examples (e.g. Maynard Smith 1978). This principle is important in cases where a correlation between a trait and a habitat factor supports a particular adaptive explanation of the trait. It is widely accepted that the proper measure of such a correlation is the number of evolutionary originations of the trait associated with the habitat, not the number of species or populations associated with the habitat. The fact that eusociality is widespread in hymenoptera is a powerful comparative argument for the view that eusociality evolved because of the unusual hymenopteran system of sex determination. The argument is powerful because eusociality has eleven separate evolutionary origins in hymenoptera. A comparable argument concerning some unusual feature of termite genetics would be substantially undermined by the fact that the many eusocial termite species inherit their eusociality from a single common ancestor.

The advocate of the exaptation concept and the conventional comparative biologist are both implicitly appealing to phylogenetic inertia to explain the continued existence of traits once they have evolved. Robert Brandon (1990, 172) seems

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to have been the first to notice that Gould and Vrba's exaptation concept suggests an implausibly strong conception of phylogenetic inertia. Elsewhere I have called this strong version of phylogenetic inertia the 'Newtonian' conception—a trait produced by a selective force continues to exist until it meets some opposing force (Griffiths forthcoming a). According to the Newtonian conception, later selective forces acting on a trait do nothing to explain its continued representation in the population. Brandon notes that this runs counter to the idea of stabilizing selection. In the absence of any selective forces favoring the existing trait, alternatives to it should enter the population by mutation and spread by drift. The inadequacy of the Newtonian picture has been noticed independently by several authors since Brandon's comment (Griffiths 1992, Reeve and Sherman 1993, Dennett 1995). An alternative 'Aristotelian' conception of phylogenetic inertia seems closer to the truth for many traits. Selection imparts a limited quantity of 'inertia'. Traits which no longer confer any advantage first become rudimentary and are eventually eliminated from the population.

The concept of a developmental constraint can be seen as an attempt to explain the 'Newtonian' phylogenetic inertia of a certain class of traits. Systematists have long been accustomed to divide traits into those which are highly conserved, and thus good systematic characters, and those which are more variable. A trait like the pentadactyl limb of tetrapods seems to have an enormous amount of inertia. The relative positions of its parts are preserved in everything from a frog's leg to a bat's wing. As this example shows, highly conserved traits are not obviously conserved by some universal selective advantage which they confer and which leads to stabilizing selection. They are nevertheless highly conserved. Developmental constraints are postulated non-selective causes of this conservation. They cause traits to resist whatever forces are responsible for the rudimentation and elimination of other traits. As well as performing this conservative role, developmental constraints are conceived as interacting with selective forces to co-determine the actual evolutionary pathway taken by a lineage.¹

2. Process Structuralism and Complexity Theory. Process structuralism is the modern representative of the 'developmentalist tradition' in biology (Depew and Weber 1995). Developmentalists downplay the role of natural selection in explaining the diversity of life. They interpret evolutionary history as an exploration of possibilities implicit in the conditions that set up the evolutionary process. According to process structuralists like Brian Goodwin and Gerry Webster,² the space of possible biological forms ('morphospace') is divided into regions characterized by particular 'generic forms'. From a Darwinian perspective, generic forms appear as traits that are highly conserved in certain lineages. According to process structuralism, generic forms result from the fundamental ways in which organisms in those lineages grow. In the case of the tetrapod limb, process structuralists appeal to a well-known model according to which all tetrapod limbs are formed by differing combinations of three processes in the limb bud—condensation of cells along a single axis, branching bifurcation and segmentation at a point along the axis (Oster, Murray, and Maini 1985; Oster et al. 1988). These rules dictate, for example, that all limb structures will begin with a single bone and that there will be no tripartite branchings. The generic forms of the tetrapod limb are compulsory for

¹The 'interactionist' picture of developmental constraints has been strongly criticised by Oyama (1992). The notion of constraint is carefully analysed by Amundson (1994).

²Goodwin 1994, Goodwin and Saunders 1989, Goodwin and Webster forthcoming. Earlier philosophical analyses of these views can be found in Smith 1992 and Van der Weele 1995.

organisms in this region of morphospace because they are dictated by very general aspects of the way in which those organisms achieve organized growth.

In recent years, process structuralism has drawn on complexity theory and particularly on the work of Stuart Kauffman (1993) to explain the stability of generic forms (Goodwin, Kauffman, and Murray 1993). Goodwin now thinks of the developing organism as a chaotic system for which the generic forms are attractors. The parameters for any particular 'run' of this system are set by the genes. Changes in these parameters will affect many aspects of the run, but rarely will enable the system to escape from the strong attractors represented by generic forms.

There are strong parallels between this recent interpretation of the developmental processes studied by structuralists and earlier conceptualizations of the same processes in terms of 'developmental canalization' (Waddington 1959). The idea of developmental canalization is that development can be buffered against genetic variation just as it can be against environmental variation. Waddington compared the developmental system to a landscape and the organism to a ball rolling down a path dictated by the contours of this landscape. A suitable landscape will take the ball to the same destination from a wide range of starting points. It is this possibility which is ignored in arguments like that of John Tooby and Leda Cosmides (1992). These authors suppose that all the alleles underlying any complex adaptation must be at fixation in a population (and hence that every individual must be identical at those loci) if the genetic basis of the adaptation is not to be destroyed during sexual reproduction! The concept of a robust developmental process which can reach the same result from a range of genetic parameter settings makes this unlikely conjecture unnecessary. In a further parallel with the vision of the complexity theorists, Waddington conceived of the developmental landscape as 'held down' underneath by individual genes. Genetic change would affect the shape of the landscape. The developmental system is simultaneously the product of the genes and the determinant of their significance.

A model of the phenomena of robust developmental pathways in complex systems theory is a promising starting point for process structuralist research. It allows the construction of increasingly realistic simulations of the developmental process. Complex systems theory thus has the potential to play the same role for process structuralism that evolutionary games theory has played for the study of adaptation. It allows substantial explorations of the idea of robust development without the enormous effort of empirically deciphering the working of real systems. Kauffman's work has provided strong theoretical support for the view that the viable region of morphospace surrounding any existing organism and containing the real possibilities for the future evolution of that organism is characterized by robust features that exist throughout the region. These features are the generic forms.

3. The Return to Ideal Morphology. Darwinism organizes the system of nature using the principle of common descent. Organisms are grouped cladistically on the basis of common ancestry. Traits of organisms are classified using evolutionary concepts of homology and analogy. Traits are homologous if they are derived from the same ancestral trait. Traits are analogous if they are responses to the same selective pressures. As David Hull has stressed, only the categories based on analogy and parallel evolution are candidates to be natural kinds in the traditional sense. Natural kinds as traditionally conceived have spatio-temporally unrestricted definitions and enter into spatio-temporally unrestricted laws of nature. Categories based on evolutionary analogy (e.g. 'predator', 'edge detector' and 'agonistic behavior') have pretensions to be natural kinds of this sort. They would enter into universal laws of ecology—the science of organism/environment interaction (Hull

1987). Unfortunately, as Aubrey remarked of astrology, 'we have not that science yet perfect'. Actual workers in systematics, developmental biology, ethology, and so forth work largely with categories based on evolutionary homology. Each trait belongs to a nested hierarchy of categories defined by series of ancestral forms. Bones in the tetrapod limb are classified as carpals because they derive from a particular element in an ancestral tetrapod limb, not because they play the same ecological role. The square-mouthed anger display in humans is classified with the subordinate threat display in the chimpanzee because they are homologues, even though the display in humans no longer seems to play the same specialized role. Darwinism finds itself espousing a scheme of classification for biological form which does not represent a system of natural kinds that could enter into scientific laws as traditionally conceived.³

The process structuralists have been quick to exploit this embarrassment and to suggest an alternative system of classification. They propose to return to something much more like the 'rational' or 'ideal' morphology of the last century. Goodwin proposes to classify traits by 'equivalence'. He places in the same category all forms that can be produced from the same resources by some limited set of developmental transformations. Classifications of greater or lesser generality can be produced by using larger or smaller sets of permissible transformations. Tetrapod limbs are not all and only the limbs derived from a common ancestor, but all and only the forms which can be constructed using the three principles of morphogenesis mentioned in the last section. Goodwin tells us: "I believe that this provides a much sounder basis for a taxonomy of forms than a genealogically based classification scheme. . . . Generative principles provide a better foundation for understanding structure than historical lineages." (1994, 154).

The process structuralist ideal is a periodic table of organisms or traits of organisms based on the generic forms. These categories enter into the laws of development that process structuralists and complexity theorists aim to discover. A new ideal for evolutionary explanation accompanies this new ideal of classification. Biological forms are to be explained by placing them in the periodic table of morphology rather than by tracing their history. Historical explanations are replaced by structural explanations. The process structuralists claim that the later form of explanation is superior because it explains form in terms of general laws rather than historical happenstance. The historical narratives associated with Darwinism are seen as true but unilluminating. Goodwin offers an explanation of the increasing asymmetrically and complexity of a lineage of fins that exemplifies the new explanatory ideal:

This is a natural progression for a dynamical system as its parameters undergo variation by random shuffling of the genetic pack. Any system which starts off simple will tend to get more complex. It has nowhere else to go. Natural selection does not have a lot to do except act as a coarse filter that rejects the utter failures. . . . The question is then: Which are the robust forms that emerge from the evolutionary exploration of the space of possible organisms? (Goodwin 1994, 157).

4. Natural Kinds and Causal Homeostasis. In the next, final section of this paper I will challenge the claim that structural explanations of the kind just outlined are genuinely explanatory. In this section I want to reject the view that Darwinian,

³The clear recognition of this fact has been relatively recent and is due in a large measure to the work of Michael Ghiselin (1974) and David Hull (1976).

historical explanations are flawed because they do not involve natural kinds. The contrast that Goodwin and others have drawn between the historical, happenstance explanations of Darwinism and their own, lawlike explanations rests on a mistaken conception of natural kinds and their role in scientific explanation.

Kinds are the clusters of properties that are essential for the practices of explanation and induction. By determining that an individual is a member of a kind we can infer its possession of properties other than those used to place it in the kind. Kinds are the realist interpretation of Goodman's 'projectible properties' (Goodman 1954). They represent correlations between properties which our background theories suggest can be relied upon to hold up in unobserved instances. The use we make of kinds requires that there be some underlying cause of the property correlations we have observed. If there is no such underlying cause then our inductive expectations are unwarranted and our explanations without force. Richard Boyd has termed these underlying causes 'causal homeostatic mechanisms' (Boyd 1989, 1991). Psychologists like Frank Keil (1989) and anthropologists like Scott Atran (1990) have tried with considerable success to demonstrate the reality of 'psychological essentialism'. People do not simply note the existence of clusters of properties. They postulate a system of underlying causes of the clustering. These theoretical claims play a central role in people's reasoning about kinds.

The mistake made by the process structuralists is to assume that a causal homeostatic mechanism must take the form of a set of essential intrinsic properties. The 'essences' of kinds have traditionally been presumed to be intrinsic, usually microstructural, properties that are causally responsible for the observable properties of their kinds. Philosophers like Hilary Putnam (1975) and John Dupré (1981) simply assume that genetic essences akin to the atomic structure of chemical elements are the leading candidates for the essences of biological species. But the concept of causal homeostasis entails a much broader conception of the 'essence' of a category. Once the actual cognitive role of essences is made clear, it is apparent that an 'essence' can be any theoretical structure that accounts for the projectibility of a category. Even the stock examples of natural kinds do not all have microstructural essences. The fundamental kinds of the physical sciences, such as the elements and categories like acids or alkalis, have their properties because of their internal microstructure. But biological taxa, the other classic example of natural kinds, have their causal homeostasis guaranteed quite differently. The most successful attempt to date to sort organisms into kinds which represent rich clusters of properties that can be relied upon to hold up in unobserved instances is phylogenetic systematics. A cladistic classification of an organism or part allows reliable inferences about its structure, development, and behavior. These inferences are probabilistic, but none the worse for that. Correlations between properties do not need to be deterministic to be useful for explanation and induction. Biological taxa at all levels of the taxonomic hierarchy form projectible categories because their members are descended from a common ancestor. Their 'essences' are historical. Taxa at the species level have rather more complex essences, because in their case these genealogical forces are supplemented by factors such as gene flow, selection, and developmental canalization (Mishler and Donoghue 1982, Mishler and Brandon 1987). I have argued elsewhere that the essences of many biological and psychological traits are historical in much the same way as the essences of the taxa that exhibit them (Griffiths 1994). A classification of traits in terms of evolutionary homology gives access to a rich cluster of intrinsic properties—richer than can be found using any other available scheme of classification. The Darwinian categories which the process structuralists disparage as unable to enter into

real laws of nature are in fact paradigmatic natural kinds which enter into robust scientific generalizations.⁴

5. Generative Entrenchment and the Shape of Morphospace. I have tried to show that the charge that Darwinian, genealogical categories are unsuitable for the central scientific activities of explanation and induction is without foundation. It may appear that in doing so I have walked straight into the arms of process structuralism. After all, to say that the causal homeostatic mechanism of kinds in biology is common descent is to invoke something like the notion of phylogenetic inertia. The claim that cladistic classifications are 'maximally predictive' (e.g., Fink 1979) is the claim that a classification of organisms or their parts in terms of current ecological role will account for relatively little of the pattern of distribution of characters when compared to a phylogenetic classification. Traits are conserved in a way that is unresponsive to immediate adaptive pressures. Isn't this exactly the phenomenon that the process structuralists used to motivate their claim that developmental constraints play a fundamental role in evolutionary explanation? The answer to this conundrum is that classifications of organisms and parts in terms of the developmental processes that produce them *are* essential to a proper understanding of evolution but that these classifications of developmental processes are in all likelihood Darwinian and genealogical. The idea of generic form can and should be historicized.

The generic forms divide the overall space of biological possibility into discrete regions available to each particular type of organism. The process structuralists view this structuring of the space of biological possibility as part of the fundamental physical structure of nature. But the phenomena of phylogenetic inertia and developmental constraint do not support this interpretation. These phenomena show that the evolutionary pathways available to an organism are a function of the developmental structure of the organism. However, nothing in the phenomena suggests the sort of manageable periodic table of organismic forms that would be necessary to make the structural explanations of form envisaged by Goodwin (1994) genuinely explanatory. The generic forms that exist in nature may be a tiny subset of the possible generic forms that could have been created by the historical design of alternative developmental systems. In that case, an explanation of the organism's form in terms of which developmental system it possesses would in no way displace the Darwinian explanation of form in terms of descent with modification. The developmental system could have been any one of a number of ways depending on the particulars of evolutionary history.

In recent years, William C. Wimsatt has written extensively about a Darwinian mechanism that could divide the space of biological possibility in the manner of generic forms. This mechanism is 'generative entrenchment' (Wimsatt 1986, forthcoming; Schank and Wimsatt 1986). Wimsatt notes that the key to natural selection is the possibility of incremental design. Very unlikely forms can be produced by a simple generate and test procedure because they can be produced a piece at a time. The improbability of the overall design is the product of the improbability of its components. These component improbabilities can be relatively small. This process of incremental design has the consequence that a later modification is generated against the background of the existing developmental system. The removal of ancient elements of the developmental system is therefore likely to remove the presuppositions of later modifications, and so to disrupt the development of those modifications. Elements of the developmental system tend to become in-

⁴This account of natural kinds is defended at more length in Griffiths forthcoming b.

creasingly generatively entrenched as more is built on top of them. The existing developmental system of the organism therefore comes to shape the space of possibilities available to the organism in its future evolution.

Wimsatt's mechanism is Darwinian through and through, yet it predicts phylogenetic inertia, particularly of structural traits, and the appearance of 'developmental constraint'. As Daniel C. Dennett (1995) has remarked, Kauffman's (1993) models of the developmental basis of 'Newtonian' traits are entirely consistent with the framework Wimsatt has proposed. Once the red herring of natural kinds is dismissed, the only reason to accept the process structuralist vision rather than a historical vision like Wimsatt's is the unmotivated presumption that the generic forms evolution has so far produced represent a significant portion of the space of biological possibility. The process structuralists assume that the space of biological possibility contains few viable regions other than those whose generic forms we see around us. The particular historical pathway by which a viable region was reached does not satisfyingly explain why organisms are found in that region rather than some other, because almost all viable regions were reached by some organism. Conversely, describing which of the very few viable regions an organism occupies provides a satisfying explanation of its generic properties. The dispute between process structuralists and Darwinists can be represented in terms of the pragmatics of explanation. The process structuralists offer a vision of morphospace which makes the question, "Why are organisms in this viable region?", suggest the contrast, "... rather than some unviable region." With that contrast in mind, the process structuralist explanation is satisfying. Darwinian explanations of form presuppose a vision of morphospace according to which the question, "Why are organisms in this viable region?", suggests the contrast, "... rather than some other viable region."

Some findings from palaeontology suggest that the process structuralist vision of morphospace is mistaken. The diversity of the fauna produced in the Cambrian explosion suggests that the space of biological possibility contains many more discrete regions of viable form than have actually been explored. Many traits picked out by process structuralists as generic forms because of their phylogenetic stability originated in one or a few species in the Cambrian explosion. Other species present at that time were anatomically highly distinct from these species. If the other species had produced rich clades of descendant species, those clades presumably would have been marked by 'generic forms' that we can now only guess at. Stephen Jay Gould (1989) has argued that these other species were merely unlucky that their descendant clades did not to make it through subsequent events of mass extinction. Whether or not this is correct, these species were obviously developmentally viable. This suggests that the process structuralist presupposition is false and that the space of biological possibility contains many viable regions that have not been explored. This in turn would imply that structural explanations of biological form would be relatively unilluminating. The statement that an organism has its generic features because it is in a particular region of morphospace begs the question of why it is in that region rather than any other. This question must be answered in terms of evolutionary history.

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