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Pluralism and Convergence in Evolutionary Theory

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INTRODUCTION

It has been more than 50 years since the neo-Darwinian synthesis began with Fisher's *Genetical Theory of Natural Selection*. In that time, it has generated a veritable industry of theoretical and experimental research devoted to explicating and demonstrating the operation of the principle of natural selection. Of late, the extension of that principle to social behaviour has given birth to the 'new science' of sociobiology which, Gargantua-like, immediately threatens to subsume both anthropology and sociology. Yet, paradoxically, just as the grand synthesis seems on the verge of being complete, it has come under scientific attack simultaneously from a number of different directions. Why should this be? Perhaps it is an expression of the *Zeitgeist* which has mysteriously captured the period; or perhaps it is simply that the time is ripe for a post-Darwinian revolution.

There have always been critics of the neo-Darwinian synthesis: independent thinkers who steadfastly refused to lose sight of the fundamental problems of evolution which the theory does not address. The most influential among the critics were undoubtedly Waddington, Goldschmidt, and D'Arcy Thompson, who did much to keep the real issues alive throughout the period of the grand synthesis. Their writings continue to inform the present evolutionary controversy, though they were not sufficient by themselves to bring that about. The precipitating factors for

the controversy were, we suggest, important discoveries made in molecular evolution and paleontology. These have led to major conceptual crises within the orthodox theory, compelling many workers to reassess its basic tenets.

The discovery that the rates of amino acid substitution in proteins are nearly constant during evolution gave rise to the hypothesis that many mutations may be 'neutral' with regard to natural selection (Kimura, 1968). This hypothesis was corroborated by the observation that abundant electrophoretic variations exist in natural populations (Lewontin and Hubby, 1966; Harris, 1966)—too abundant in fact to be accounted for by natural selection. The conclusion seems inescapable that the majority of genetic variations are of no physiological or phenotypic consequence. Indeed, the general disparity between genic and organismic evolution which soon emerged suggested an effective decoupling between the two. The best known example is provided by the finding that humans and chimpanzees, which are biologically so distinct as to be classified in different families, nevertheless are 99 per cent identical in their genes (King and Wilson, 1975). Such observations prompted us and others to question the validity of a theory of evolution that is essentially based solely on genes. The neutral mutation concept represents an important turning point in the history of ideas. It presaged the fall from dominance of the genetic theory of natural selection—and the concomitant return of theories on organismic structure and form.

Concurrent with the developments in molecular evolution, the Darwinian picture of gradual phyletic transformation of species was being slowly and surely eroded by improved stratigraphic analyses of the fossil record. The latter soon appeared to confirm earlier speculation of paleontologists such as Schindewolf that the postulated continuous series of intermediates during species transformations simply do not exist. Hence the origin of species may require other explanations than those offered within neo-Darwinian orthodoxy (Eldredge and Gould, 1972).

While the above discoveries and their consequences were crucial, they were precipitating factors only. For the evolutionary controversy which ensued is wide-ranging in scope. Development and the nature of the organism rapidly come to the fore as problems unintelligible within neo-Darwinism. Long cherished dogmas of heredity on which neo-Darwinism is firmly based, are being challenged from within molecular biology itself. The science of systematics and rational morphology, after a century of eclipse under the Darwinian dictum of 'descent with modification' has finally come into its own again, overturning deeply held assumptions in phylogenetic classification.

The present intellectual 'uprising'—a cross-section of which is represented

in this volume—is unique. It springs simultaneously and independently out of diverse disciplines: from chemists contemplating the origin of life to developmental psychologists preoccupied with the origin of human nature. At first glance, they seem to have little in common save a dissatisfaction with the neo-Darwinian framework. A closer inspection reveals the connecting threads which converge on those fundamental issues of evolution left largely untouched by Darwin and his followers. Problems such as determinism and direction in evolution, global patterns of speciation and extinction, and the origin of biological form and function, have been regarded by neo-Darwinists either as irrelevant—because they are outside the scope of the theory—or as explicable by natural selection in combination with different *ad hoc* assumptions. To us, on the other hand, these problems are primary to evolution, and hence epistemologically prior to natural selection. Our common goal is to explain evolution everywhere by necessity and mechanism with the least possible appeal to the contingent and teleological. Accidental variation and selective advantage—the foremost categories of explanation in neo-Darwinism—are thus relegated here to the last resort.

It must not be supposed however, that there is anything approaching the ‘consensus’ which is often claimed for the neo-Darwinian synthesis. Pluralism is a predominant feature of the emerging paradigm of evolution. Not only is there a genuine (and in our view, healthy) diversity of opinion and emphasis, but evolution is a complex phenomenon and it is to be expected that different kinds of explanations will be appropriate to different aspects. In particular, higher level explanations cannot always be collapsed or reduced into lower level ones. Thus, pluralism ought in principle to be a permanent feature of evolutionary studies.

Above all, however, our emphasis is on process—surprisingly rich and varied in texture seen from different vantage points. The result is a transcendence of the predominantly Aristotelian framework of neo-Darwinism—in which organisms are explained in terms of essences or genes—to the post-Galilean world view in which relation and process are primary. Perhaps this is but part of the general scientific revolution that has been long overdue in biology.

RANDOMNESS AND DETERMINISM

The neo-Darwinian concept of random variation carries with it the major fallacy that everything conceivable is possible. This is made most explicit in discussions on the origin of life, when it is claimed that life is utterly

improbable without natural selection. The argument is usually couched in terms of the probability that a functional polypeptide of a *specific* amino acid sequence could arise by chance, which is vanishingly small, if one supposes that all conceivable random sequences of 20 amino acids are equally likely to occur. Now, the latter supposition contains the false assumption that we have a universe of pure numbers devoid of physics or chemistry. In fact, experiments under simulated prebiotic conditions consistently tell us that the probability space of prebiotic proteins is much more restricted (Fox, Chapter 2).

The same experiments show that the other assumption implicit in such formulations—that *function* is a very rare and special quality created only as the result of natural selection—is also false. Proteinoids synthesized in the laboratory already possess a variety of catalytic functions. This is indeed a vindication of Henderson's (1913) thesis of the 'fitness of the environment'. The Darwinian notion that organisms are fitted (or adapted) to the environment is incomplete, for it misses the reciprocal in the relationship: the environment is fit for the origination and evolution of organisms. Ultimately, mechanism and teleology may be one and the same, being part and parcel of the properties of matter of which living things are composed.

Inherent in the idea of non-randomness and material self-organization (Fox; Matsuno, Chapter 3) is the concept of determinism in evolution. This is best expressed by a quotation from T. H. Morgan (1929), founder of chromosomal genetics:

When, if ever, the whole story can be told, the problem of adaptation of the organism to its environment and the coordination of its parts may appear to be a self-contained progressive elaboration of chemical compounds—a process no more fortuitous than the constitution of the earth or its revolution about the sun. The outcome would be as determined as any natural event, subject always to the principle of survival . . .
(p. 77)

Determinism in turn implies a general direction or 'time's arrow' in evolution. Many recent attempts have been made to identify a relatively objective quality if not quantity which increases in evolution; one suggestion is 'complexity' (see Saunders and Ho, 1976). Wicken (Chapter 4) attempts to account for the increase in complexity in evolution from a thermodynamic perspective: the second law promotes chemical structuring through the randomization of potential energy and material configuration. This is reminiscent of Joseph Needham's (1943) earlier attempt to reconcile the apparent contradiction between the increase in entropy predicted by the second law and the increase in biological organization in evolution. Wicken and Matsuno both envisage an inexorable impetus for evolutionary change: the former in the flow of energy along ordered pathways of entropy

production, the latter in the flow of material through self-organizing systems. For Wicken, the evolutionary 'motor' is cosmic energy external to the biosphere, whereas for Matsuno, it is the process of equilibration endogenous to self-organizing systems which incessantly gives rise to further evolution autonomously.

PATTERNS OF ORGANISMIC EVOLUTION

If deterministic constraints exist, then certain regularities or trends in the large scale pattern of evolution should be evident. Yet very few studies have addressed this problem. One main reason is that natural selection is strictly a local mechanism (Saunders and Ho, 1976) and hence inherently unable to account for any global trend or pattern (Vrba, Chapter 5). Another reason is that evolutionary pattern itself is the product of inference from available data. Where inference is habitually made under certain presumptions, the resulting pattern becomes correspondingly biased. A case in point is the phylogenetic classification of organisms.

Organisms exist in a naturally ordered hierarchy, and it is that which makes a hierarchical system of classification possible. This is independent of the Darwinian notion of descent with modification, as the success of pre-Darwinian systematics amply demonstrates. But when phylogenetic classification is performed under presumed adaptive pathways, as implied by Darwinian natural selection, pattern becomes confounded with hypothetical process. Cladistic analysis is an attempt to re-dissociate inferences of organismic relationship and evolutionary pattern from assumptions concerning process (Nelson and Platnick, Chapter 6). The first results of its application already present views of evolution very much at odds with the orthodoxy.

The predominant pattern of the fossil record is punctuated equilibria: long periods of relative stasis interrupted by bursts of speciation events at which almost all morphological divergences take place. Many interpret this to be an indication that the process occurring within species (neo-Darwinian micro-evolution) differs from that which establishes species (macro-evolution, Vrba). Biogeographical data begin to yield families of species relationships which are congruent for widely different groups inhabiting the same areas. This implies the existence of historical geological events which subdivide geographic areas, resulting in parallel paths of divergence for all included groups of species (Nelson and Platnick). Orthodox explanations based on centres of dispersal of ancestral taxons are thus called into serious question.

The significance of the above observations lies not so much in their obvious challenge to established ideas as in their demonstration of how the arbitrariness of description of data can be reduced. This allows the proper integration of phylogenetic data, paving the way to more rigorous formulation and testing of evolutionary hypotheses concerning process.

THE PROBLEM OF FORM

The abstraction of empirical regularities or patterns is not enough, however. The regularities of biological form have been extensively commented on by students of morphology since Goethe's hypothesis of the 'unity of type'. Yet only relatively recently have there been attempts to look beneath the regularities for the *generative* germs of form (Webster, Chapter 8).

Pre-Darwinian morphologists like von Baer, Geoffroy St. Hilaire and Richard Owen clearly perceived a deep connection between the systematics of natural forms and the organization of developmental processes by which forms are realized. Since Darwin, this connection has been interpreted purely in terms of descent with modification. Organisms are seen to be the sum of past random variations accumulated by natural selection and preserved by heredity. Form therefore requires no other explanation than a combination of utility and historical contingency. Similarly, development (or ontogeny) is nothing more than the recapitulation of evolutionary history (or phylogeny). Such was the basis of Haeckel's famous biogenetic law.

But organisms are not preformed in the germ, they take shape epigenetically, in the course of development. As von Baer noted long ago, the regularities of ontogeny point to the existence of an underlying universality of process independent of recapitulation. Thus, the cause of phylogeny may be sought within the epigenetic processes involved in ontogeny itself (Løvtrup, Chapter 7). Løvtrup indeed interprets cladistic phylogenetic trees literally in the sense that the evolutionary pathways—or pathways of changes in ontogeny—can be read off directly from them. The corollary of this is that ontogenetic sequences can be used to test phylogenetic hypotheses (Nelson, 1978). At any level of a phylogenetic hierarchy, primitive (plesiomorphic) characters should be common to the ontogenies of two or more groups, and derived (apomorphic) characters should be group specific.

The thesis that development exerts deterministic influence on evolution is assumed by many authors: it is certainly a strong underpinning of

contemporary evolutionary thinking. However, there is a clear divergence in emphasis as to the precise nature of the developmental 'constraints' on evolution.

The major divide is a diachronic-synchronic one. At the extreme synchronic level, catastrophe theory defines a taxonomy of pure forms which is independent of the substrate (Thom, 1972). This has the important implication that all, or nearly all dynamical systems may be reducible to a limited number of canonical classes. At once, it becomes tempting to consider if the multifarious array of biological forms could be described in terms of combinations of the elementary catastrophes in such a way as to constitute a 'theory of archetypes'. This would be an extremely ambitious undertaking even if it were feasible in principle, as there are layers of analysis yet to be performed before empirical observations and abstract theory could be bridged. Granted that there might be a structuralist core of 'invariants' to biological forms, would that adequately describe much that is of interest and relevance in evolution? It might well be that the historical and functional contributions to biological form are as considerable as the purely structural. To paraphrase Polanyi's aphorism, 'mathematics is dumb without the gift of boundary conditions'.

In the intermediary realm between empirical observations and abstract forms we find several levels of theorization concerning the origin of spatial organization (Saunders, Chapter 10)—the fundamental problem in development. The aim is to generate spatial heterogeneity from a relatively homogeneous state. A variety of models demonstrate the extent to which mathematics, physics and chemistry can contribute to the genesis of specific forms—a project initiated by D'Arcy Thompson (1917). Constraints to form thus arise as natural necessity rather than from natural selection. The major evolutionary consequence is that it is dynamic expediency and not selective advantage which may largely determine evolutionary pathways, and hence phylogeny.

At a higher level of analysis we find Goodwin's field theory description of development (Chapter 9). The concept of fields dates from the great embryologist Hans Driesch (1892). It derives from the phenomenon of regulation—the reconstitution of developmental fields of whole organisms from material parts of early embryos—which has consistently resisted assimilation into the dominant genetic theory of development. (Ho, Chapter 11, argues for the necessary independent localization of field or field-like properties in the egg cytoplasm as the means of 'translating' one-dimensional 'instructions' in the genes to the 3-dimensional spatial domain of the organism.) Goodwin identifies general processes within which detailed mechanisms could be coordinated. The articulation of process is independent of the description of underlying mechanisms, however (see

Boden, Chapter 13); in particular, the latter does not translate directly into the former. Thus, the overwhelming diversity of molecular mechanisms recently uncovered by recombinant DNA technology has contributed little apart from puzzlement to our understanding of the process of development (Dawid, 1982). This speaks most eloquently against any claim that organisms, and perforce, societies and cultures, can be reduced to molecules and genes. In order to flesh out our understanding of nature, we must apprehend the unity of process at the intermediate levels of generality between mechanisms and pure form. The field theory description can be seen as an attempt to fulfil that role. At the same time, it is also capable of addressing the diachronic aspect of evolution in the 'internalization of constraints' of which more will be said below.

DESIGN AND FUNCTION

It is perhaps significant that the inventor of catastrophe theory himself is not a pure structuralist. He has this to say about evolution (Thom, 1968): '... I believe that in biology there exist formal structures ... which prescribe the only forms which a dynamic system of autoreproduction can present *in a given environment*.' (italics ours)

Thus, an organism is not uniquely defined unless its environment is specified. The relationship between an organism and its environment constitutes its functions or adaptations. Ho (Chapter 11) argues that organism-environmental interactions contribute to the genesis of form via an essentially Lamarckian process of canalization and genetic assimilation (or 'internalization') of experienced environments. In a similar vein, Pollard (Chapter 12) reviews the extraordinary diversity of recently discovered molecular mechanisms which can render Weismann's barrier permeable to environmental influences, especially of the kind involving the transfer of nucleic acid coded information. Preoccupations such as the above with the origins of adaptive molecular functions or morphology, as well as behaviour (Sinha, Chapter 14) give emphasis inevitably to the diachronic aspect of evolution.

It is impossible—certainly at present—to state how much of biological form is due to structural considerations and how much to functional considerations. Perhaps it would not be out of place to suggest that from the functionalist perspective, evolution is emergent or creative. This is not to say that evolution is indeterminate, only that it is not *finalistic*. In fact, it is only by virtue of the structural (deterministic) core that organic systems can exist which can in turn assimilate and evolve to further novelty and

complexity. Thus, epigenetic systems, like representational systems in psychology (Boden; Sinha) are neither synchronic nor diachronic, for structural and functional constraints are inextricably interwoven. (This view is broadly compatible with those of Fox, Wicken, and Matsuno for the evolution of the biosphere as a whole.)

THE UNIQUENESS OF THE HUMAN SPECIES

The applicability of Darwinian natural selection to the evolution of the human species has been strenuously debated since Darwin's days. The usual answer to Social Darwinism is to appeal to the uniqueness of our species—our social, cultural and mental attributes—which somehow override our genetic biological heritage. Such arguments are without force, for it is precisely those social, cultural and mental attributes that the present day counterpart of the Social Darwinists—the sociobiologists—claim to explain in terms of the genetic and biological.

Both sides in the debate suffer from the inherently fallacious, but unquestioned assumption that all or almost all of evolution can be explained by the natural selection of random mutations. Once we go beyond the restricted framework of neo-Darwinism there is indeed no need to deny our biological heritage, nor need we shun the study of such characteristically human attributes as the mind (Boden). Artificial intelligence allows the exploration and illumination of natural intelligence. It provides a description of the mental process which is irreducible to molecules and detailed mechanisms; thus emphasizing the richness and subtlety of that process.

But mind, like organism, arises epigenetically (Sinha). The social environment enters as formative influence into development. Perhaps human freedom and uniqueness lie precisely in that responsibility for an environment in which our species can develop and evolve.

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