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978-0-521-20743-0 - Form and Transformation: Generative and Relational Principles in Biology

Gerry Webster and Brian Goodwin

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Organisms have disappeared as fundamental entities from modern biology, replaced by genes and their products as the primary determinants of selected characters. This is a consequence of Darwin's theory of descent with variation and survival of fitter variants. The first part of this book (by Gerry Webster) looks critically at the conceptual structure of Darwinism and describes the limitation of the theory of evolution as a comprehensive biological theory, arguing that a theory of biological form is needed to understand the structure of organisms and their transformations as revealed in taxonomy. The second part of the book (by Brian Goodwin) explores such a theory in terms of organisms as developing and transforming dynamic systems, within which gene action is to be understood. A number of specific examples, including tetrapod limb formation and *Drosophila* development, are used to illustrate how these hierarchically organized dynamic fields undergo robust symmetry-breaking cascades to produce generic forms. These are the basic morphological structures available for evolutionary transformations, whose classification into equivalence classes provides a basis for taxonomic relationships.

Evolutionary and developmental biologists, geneticists and philosophers of science will all find this a thought-provoking book.

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Generative and Relational Principles in Biology

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Frontmatter

[More information](#)

Contents

<i>Preface</i>	<i>page</i> ix
<i>Acknowledgements</i>	xiii
Part I – The Problem of Form	
1 Introduction: Forms and Kinds	3
2 The Old Dialectic: Empirical Classification and Darwinian Theory	13
3 The Ontological Status of Taxa: Material Practice	40
4 The Ontological Status of Taxa: Theoretical Practice	62
5 Rational Systematics and Morphogenetic Theory: A New Dialectic?	101
Part II – Fields and Forms	
6 Putting the Organism Together Again	131
7 Segments, Symmetries and Epigenetic Maps	154
8 The Unitary Morphogenetic Field	193
9 A Generative Biology	231
<i>References</i>	257
<i>Index</i>	273

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[More information](#)

Alle Gestalten sind ähnlich und keine gleichet der andern,
Und so deutet das Chor auf ein geheimes Gesetz.

(All forms are alike and none is like another,
So that their chorus points the way to a hidden law.)

– Goethe, “*Die Metamorphose der Pflanzen*”

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Frontmatter

[More information](#)

Preface

In a summary of his discussion of morphology in the *Origin of Species* Darwin concludes that “On this . . . view of descent with modification, all the great facts in morphology become intelligible” (1859, p. 433). This book is a contribution to that tradition in biology which disputes this conclusion.

We argue that the theory of evolution provides only limited insight into the problem of form as regards both the causal explanation of form and the relations between forms. We suggest that what is required is the development of a specific causal–explanatory theory of form, a theory of morphogenesis in the most comprehensive sense, and that such a theory will be as fundamental to biology, if not more so, at least as the theory of evolution. We contest the current view that such a theory is merely a supplement to the theory of evolution and, consequently, that it should be couched in terms of a ‘genetic programme’. The end result of such a position is the disappearance from biology of organisms, conceived as fundamental and specific kinds of entities; and, to a considerable extent, this is precisely the current situation. By contrast, we argue that organisms should be regarded as the fundamental entities of biological theory. Following scholars such as Needham, Waddington and Woodger, we argue that a satisfactory theory of morphogenesis cannot be based upon an atomistic and mechanistic view of the organism but requires the development of a more adequate ‘Concept of the Organism’ in which organisms are treated as specific kinds of things. We advance a field theory of morphogenesis in which organisms are conceived as entities which, by virtue of their structure, are possessed of distinctive and specific generative powers, that is, natures.

Part I, written by Gerry Webster, is concerned with conceptual problems and, in particular, with the possibility of a *scientific* explanation of morphological diversity and individual forms, which was the goal of pre-Darwinian “Rational Morphology” as reconstructed by Hans Driesch. A science of form

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Frontmatter

[More information](#)

presupposes that particular forms can be conceived as instances of natural kinds; hence, the ontological status of taxa is a central issue. Evolution theory was developed, in part, as a response to the classificatory or taxonomic problem of variation, and the theory claims that individual organisms are not only related genealogically as a matter of fact but that this is the only way they can be related. Consequently, it rejects the traditional view that species (and other) taxa are classes – hence putative natural kinds – of which individual organisms are members, and replaces it with a view of species taxa as individuals – wholes – of which individual organisms are parts. Thus, if the theory of evolution is taken as providing a general metaphysical foundation for biology, it appears that there is no possibility of a scientific explanation of morphology; particular forms can only be explained by means of historical narrative, and the diversity of forms can only be unified in terms of historical genesis. In Part I, therefore, the task is, firstly, to analyse this evolutionary view and, secondly, to determine whether some view can be developed which resembles the traditional view but is free from those defects which make an evolutionary metaphysics appear attractive. Part I outlines the traditional view and considers the dialectic between empirical classification and Darwinian theory, thereby showing how the current view of the ontological status of taxa has come into being. It then considers the current view in relation to material and theoretical practice in biology. Here it is argued that this view cannot adequately sustain taxonomic and experimental practice and provides an inadequate basis for developing an explanatory theory of form. In the final chapter of Part I, an alternative dialectic is proposed between a rational systematics, of the type mooted by Driesch, and a field theory of morphogenesis.

Part II, written by Brian Goodwin, explores the structure of a theory of biological form in terms of organisms as fields. It begins with a critical look at current theories of development which are based on Weismann's separation of organisms into a genetic essence (now called a genetic programme) and a derived soma. These are examined in relation to experimental evidence and found to be inconsistent with it. Treating organisms as unified, though hierarchically complex, dynamic fields suggests a way of handling the evidence consistently. Homology emerges from this treatment as a crucial concept relating development to taxonomy, and a general definition of homology based upon developmental dynamics is proposed that has the logical structure of an equivalence relationship as used in mathematics. This is independent of history (genealogy) so that a purely relational order begins to emerge from the study of similarities and differences of organismic form at any level of the biological hierarchy, whether between parts of one organism or between organisms belonging to different taxa, independently of their genealogies.

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Frontmatter

[More information](#)*Preface*

xi

This theme is developed in relation to a variety of morphogenetic processes in different types of organisms – unicellulars, multicellular plants and animals – to illustrate how the morphogenetic field concept provides a systematic theory for the study of biological form and transformation as revealed in evolution. The hierarchical nature of biological taxonomies can be naturally related to a basic characteristic of morphogenetic fields: during the developmental process, complex morphology emerges from initially simple forms by a cascade of symmetry-breaking bifurcations that is hierarchically organised. From this comparative study emerges the basic concept that morphogenesis is an intrinsically robust dynamic process. Organismic morphologies are then predominantly expressions of the generic modes of this generative process. In consequence, morphological species are defined by generic forms, which are natural kinds rather than historical individuals, their status in Darwinism. The task then is to study and classify the stable modes of organisms as dynamic fields which include genes, epigenesis and environmental factors. This provides the basis for a theory of morphology and taxonomy in terms of the hierarchy of morphological equivalence classes defined by the transformation sets of morphogenetic fields and their attractors.

The final chapter is an initial exploration of the structure of a generative biology, one based upon organisms as the fundamental generative units of biological form. Here a link is made with new developments in the sciences of complexity, with its emphasis on emergent order from particular types of dynamic complexity, which is the natural context for the construction of a scientific theory of form and transformation.

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[More information](#)

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Gerry Webster

The concepts developed in this book arise from interaction and reflection with a great variety of people, extending back to my PhD studies in Edinburgh under C. H. Waddington, and before that as a student at McGill University with N. J. Berrill, both of whom knew William Bateson and D'Arcy Thompson. There is a kind of intellectual lineage here with a common theme centred on the problem of biological form, with diversity understood in terms of transformation. So history *does* have a role to play after all, and I ac-

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Gerry Webster and Brian Goodwin

Frontmatter

[More information](#)

xiv

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Brian Goodwin