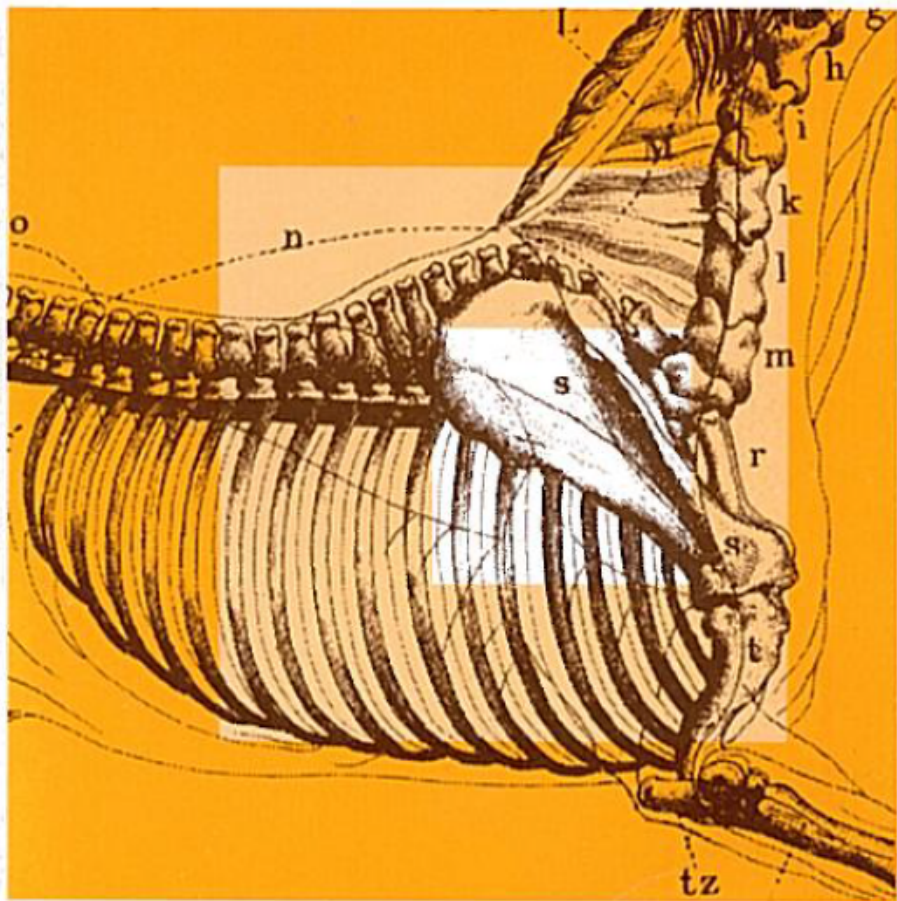


E. S. Russell

With a new Introduction by  
George V. Lauder

# FORM AND FUNCTION

A Contribution to the History of  
Animal Morphology



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## INTRODUCTION

THE discipline of morphology is currently undergoing a renaissance in evolutionary biology. After a long period of post-Darwinian dormancy, comparative morphology has emerged at the center of many active areas of research and controversy and promises to contribute new and significant theoretical concepts to our understanding of evolutionary patterns and processes. Recent discussions about rates of evolutionary change, the nature and extent of adaptation to the environment, methods of phylogenetic reconstruction, the role of epigenetic processes in evolutionary morphology, and the relationship between molecular and morphological patterns of structure have thrust the analysis of organismal form into the limelight. New methods of analyzing form and function have helped to spur this renewed interest in morphology. We can use biochemical techniques and computer models of shape transformation to make more precise studies of changes in structure during development, and the "paradigm method," constructional morphology, theoretical morphology, and functional morphology are some of the varied conceptual approaches that have become popular over the past fifteen years.

In the context of this resurgent interest in form and function, it is particularly appropriate to reissue E. S. Russell's magnificent analysis of the history of morphology. Russell's *Form and Function* (1916), subtitled *A Contribution to the History of Animal Morphology*, is a superb synthesis, tracing the history of thought on the relationship between form and function from the time of Aristotle to the early post-Darwinian era. The book is all the more valuable for its explicit antimechanistic approach, which provides considerable insight into the way

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early twentieth-century morphologists viewed the effect of Darwinism on their discipline. Russell's clarity of expression, his nearly exclusive use of primary sources, and his masterful command of the subject matter resulted in a book that "largely defined its field and by so doing made intelligible a vast amount of otherwise confusing and seemingly unrelated biological study" (Coleman 1977, p. 168). Nowhere else can one find such a lucid account of Aristotle's views on the relationships between the parts of organisms, German transcendental anatomy, and Roux's developmental mechanics woven into a theme of form versus function. Russell explained in his Preface that his aim was "to call attention to the existence of diverse typical attitudes to the problems of form, and to trace the interplay of theories that have arisen out of them." In his view, the different schools contended mainly over "the problem of the relation of function to form. Is function the mechanical result of form, or is form merely the manifestation of function or activity? What is the essence of life—organization or activity?"

This theme, the primacy of form or function, is the main thread running throughout the book. Russell delimited three major approaches to morphology, each of which has had prominent adherents. The functional or synthetic view, which sees function as the primary determinant of form, was held by Cuvier and Aristotle. A major goal of this approach was to discover principles of structural design, and Cuvier's principle of correlation (see p. 35) is perhaps the best-known example. The formal or transcendental conception of organic form held that unity of plan among organisms was the guide to analyzing morphological diversity. Function followed form, and constraints of *bauplan* imposed an "iron limit" on the adaptation of organs to functions. Materialism, the third attitude toward form, was prevalent in the early twentieth century. Russell rejected both materialism and formal morphology in favor of a Lamarckian functional view, in which the activities, responses, and needs of organisms are central concepts.

*Form and Function* has not been widely cited and was eclipsed by two of Russell's better-known works, *The Behaviour of Animals: An Introduction to its Study* (1934) and *The Directiveness of Organic Activities* (1945). In his history of comparative anatomy, Cole (1949) fails to cite *Form and Function* in spite

of his reliance on secondary sources. Nordenskiöld (1928) does not mention it. Even Agnes Arber (1937) and R. S. Lillie (1945), who held similar views on morphology and conceptual issues in early twentieth-century biology, do not refer to the book. Only in the past fifteen years have morphologists turned to Russell's study with more than a passing interest in its content, and his book is probably more widely known today than it was during his lifetime.

The general neglect that followed the publication of *Form and Function* contrasts sharply with the reception of D'Arcy Thompson's *On Growth and Form* (1917), a book published only one year later. This work was widely heralded as a milestone in the study of form, an innovative and imaginative attempt to place the study of form within the bounds of mathematics (by grid analysis of shape transformation) and physics (by explaining organismal form as the direct product of environmental action). *On Growth and Form* fit well into the mechanistic emphasis in morphological and embryological research in the first twenty years of this century.

In contrast, Russell's *Form and Function* focused on history, advocated a view of the organism as an "active, living, passionate being," and contained noticeable antimechanistic undertones. The journal *Nature* in its (unsigned) December 21, 1916, review of *Form and Function*, chose as the title of the review "Morphology: Old and New." The work was praised as "scholarly and thoughtful" and a "masterly book." But the reviewer clearly suggested that Russell's concept of history, organism, and activity (function) were not congruent with the mechanistic emphasis of active contemporary biologists. (*On Growth and Form* was reviewed one year later in *Nature* under the title "Foundations of Bio-physics.")

Russell has been a neglected figure in the history of morphology, and his many contributions to the history and philosophy of biology have not been adequately appreciated. This Introduction will consider *Form and Function* within the context of both Russell's other work and concepts and approaches to morphological research in the twentieth century. *Form and Function* can stand on its own as a remarkable history of concepts and discoveries in the study of organic form and needs no interpretational beacon. The book is largely free



of the strongly vitalistic and holistic notions that Russell championed after 1920 and is a clear and concise guide to past morphological thought. Russell expressed many of the underlying themes and concerns of this book more clearly in his later papers, and several of these topics are particularly appropriate to evolutionary morphology today.

### E. S. RUSSELL AND HOLISTIC MORPHOLOGY

E. S. Russell (1887-1954) made major contributions to the history and philosophy of biology, the study of animal behavior, and to fisheries biology. Russell's interest in the history of biology began early. In his mid-twenties, he composed a series of papers on aspects of theoretical biology that served as preliminary studies for *Form and Function* (see the bibliography of Russell's papers at the end of this Introduction).

But Russell was not a practicing morphologist, and only his very first papers—on a new genus of hydroid and the growth and structure of limpets in relation to the environment—dealt directly with morphological subjects. For most of his professional life, he worked on the day-to-day problems of fisheries management and ecology. He was associated with the Ministry of Agriculture and Fisheries in Great Britain from 1910 to 1947, and after 1921 was its director of scientific investigation (Hardy 1955 and Graham 1954*a, b*).

Russell also worked in areas other than fisheries biology, and after the publication of *Form and Function*, he pursued the directions charted in the closing passage of that book.

Dynamic materialism and dogmatic theories of evolution have in the past tended to blind us to the complexity and mysteriousness of vital phenomena. We need to look at living things with new eyes and truer sympathy. We shall then see them as active, living, passionate beings like ourselves, and we shall seek in our morphology to interpret as far as may be their form in terms of their activity.

In his subsequent three books and numerous papers on the history and philosophy of biology, Russell expanded on these



views and, beginning with his 1923 paper "Psychobiology," developed his "functional" or "psychobiological" approach to the study of organisms. He adopted this perspective as an alternative to what he regarded as the excessively mechanistic outlook of early twentieth-century biology. The central concepts of the psychobiological method, which was carefully distinguished from vitalism, were the unity and wholeness of the organism, the striving toward an end ("which constitutes the inner reality of all life" [Russell 1924*b*, p. 56]), and the integration of form and function.

Russell's antimechanistic vision pervades his work, but perhaps it is most clearly expressed in two passages of his article on the limitations of analysis in biology (1933).

If we insist on fitting life to the Procrustean bed of mechanism, we must perforce lop off its head and its feet, and content ourselves with studying the truncated corpse. (p. 150)

It is only by accepting the obvious fact that the living thing is an organized whole . . . that biologists can . . . escape the Scylla of materialism on the one hand and the Charybdis of vitalism on the other. (p. 158)

These strong views colored Russell's description of the three most active areas of biological research in the early part of this century: heredity, physiology, and developmental mechanics. He suspected conceptions that reduced an organism to isolated functioning parts and objected to gene theory precisely for this reason. The gene theory was not, first of all, a theory of development. Genes could at best be correlated with phenotypic traits and did not explain the harmony of structure and function within organisms. Moreover, particulate theories of heredity ignored history. Russell pursued this consideration down to the supposed control of cell function by chromosomes, and his holistic outlook precluded the possibility that a particulate entity like the chromosome could regulate the individual.

He combined a holistic view of heredity with a belief in the importance of goal-directed striving by organisms to achieve their needs. These ideas suggest a Lamarckian interpretation of biotic patterns that Russell in fact accepted. In his last monograph, completed in 1954 (but published posthumously in

1962), he examined possible mechanisms for the adaptive radiation of decapod crustacea. He rejected natural selection on the grounds that "only a directive and coordinated change" could explain evolutionary diversification and the finding that many crustacean lineages were "separated by characters which apparently have no adaptive value." Instead, he proposed that transformation occurred through the psychobiological process of response to need in which there was "a transmission of a psychological nature" from generation to generation. Russell quietly championed his Lamarckian view of evolution in his last paper, although he admitted that the inheritance of acquired characters was an "unproved and improbable hypothesis."

Russell subjected mechanistic theories of physiological function and development to many of these same criticisms and found fault with the attempts of Roux and His to explain change in form at the level of physicochemical interactions. He objected that "it is impossible to fragment the living organism into lower units, to ignore the problem of composition or wholeness, and to ascribe to the units the powers and capabilities which we know only as belonging to the organism as a whole" (Russell 1930, p. 49). His argument is tantamount to a claim that the internal organization of organisms is hierarchical, that there are levels of structure and activity, a thesis that is increasingly common in recent discussions of evolutionary theory.

Between 1932 and 1947, Russell was Honorary Lecturer in Animal Behaviour at University College, London (Hardy 1955), and from his lectures came *The Behaviour of Animals: An Introduction to Its Study* (1934). During the 1930s, Russell concentrated on animal behavior as a subject that illustrated clearly the goal-oriented nature of organisms and the importance of "psychological factors" to an understanding of their activity. He devoted his 1934 presidential address to the zoology section of the British Association for the Advancement of Science to "the study of behaviour" (Russell 1934c), and his three presidential addresses to the Linnean Society of London focused on various aspects of interactive behavior (Russell 1941, 1943, 1944).

Russell laid the groundwork for his analysis of behavior in his papers on psychology and biology (1923b, c) and in *The*



*Study of Living Things: Prolegomena to a Functional Biology* 1924. In this work, he intended "to outline a method for the study of living things which is neither materialistic nor vitalistic, but renders possible . . . the elaboration of a truly autonomous science of life, a real biology." He scrutinized three approaches—the morphological, physiological, and vitalistic—and rejected all three in favor of the psychobiological perspective. He viewed organisms as centers of individualized activity guided by perception. An organism's perception of the external environment and its consequent response became signal features of Russell's functional biology. But despite disclaimers, his psychobiological method often had a vitalistic resonance: "Traffic with the environment is the sole method by which the living thing can fulfil its embodied purpose of self-development and self-perpetuation, can give expression to the *élan vital*, which is the driving force of all life (Russell 1924*b*, p. 83)."

In the 1934 book on animal behavior and in more detail in *The Directiveness of Organic Activities* (1945), Russell emphasized the goal orientation that animal patterns exhibit. "When we study behaviour . . . we must ask first of all, *what is the animal doing, or trying to do?* This means that we must investigate the objective intention of its acts, the end to which they are leading, the end which satisfies them and brings them to a conclusion." He seized on directive activity as the prime argument against the Cartesian concept of the animal-machine. His approach recalls J. H. Woodger's (1930) comment in opposition to the mechanistic approach: "Has anyone observed a machine that was capable of evolution *without a mechanic?*" For Russell, directiveness was an "irreducible characteristic of life." "We must," he thought, "simply accept the immanent teleology of organic activities as, so to speak, the basis or background of our biological thinking." The maintenance of homeostasis furnished him with numerous examples of directive activity by organisms, and he adduced wound healing, the regulation of body temperature, and metabolic controls as additional evidence of directive activities serving to maintain functional integrity.

After his retirement from the Ministry of Agriculture and Fisheries, Russell extended his concept of directiveness from its initial application in problems of development and behavior to consider the evolutionary transformation of form. He con-



cluded his study of decapod crustacea by suggesting that understanding the origin of structural diversity must involve,

in addition to the Darwinian and Lamarckian factors, a mode of evolutionary change which is directive and unified, occurs at an early stage in ontogeny, and is cumulative from generation to generation. It brings about structural modifications of considerable magnitude, and not merely alterations in the degree of development of superficial characters. Such ontogenetic and aromorphic\* changes are in the main internally determined, the "initiative" to change coming from within. (Russell 1962, p. 136-37)

#### FOUR THEMES IN MORPHOLOGY

That Russell's *Form and Function* is as timely today as it was when it was published is in a large measure due to the persistent problems facing morphologists as they try to explain organic form. *Form and Function* demonstrates the antiquity of many issues being debated today. For example, the notion that extant organismal forms are only a subset of the range of theoretically possible morphologies (referred to as theoretical morphology; see Raup and Michelson 1965; McGhee 1980) can be found in the writings of Cuvier. As Russell pointed out, "if any form of any organ could exist in combination with any form of all the others there would be an enormous number of combinations theoretically possible" (p. 33). Only those forms exist that meet the conditions existing in nature, and actual morphologies fill only a portion of a theoretical "morphospace."

Theoretical morphology addresses but a part of a larger issue, the problem of morphological diversity. Russell shows that this diversity and attempts to classify it were central concerns of pre-Darwinian morphologists. Furthermore, these classifications were motivated not only by a desire to find a natural grouping of living things based on similarities in structure, but also by recognition of the apparent functional

\* Aromorphosis, one of Severtsov's "laws of evolution," is the increase through time in structural or functional complexity, and general adaptation to the environment (Adams 1980).

harmony of organic design. Thus, while the concept of unity of plan allowed forms to be classified on the basis of structural similarity, principles of functional organization were used to explain why organic form had the structure it did, the relationship of form to environment, and physiological differences between organisms. In *Form and Function* Russell lucidly examines several of these principles: division of labor between parts of an organism, the correlation of parts, and the repetition of segments and structures and its effect on design. These concepts, which Aristotle, Cuvier, Geoffrey, and Goethe recognized as central to an understanding of organic form, are still important today as morphologists attempt to explain the transformation of design and the relationship of form to the environment.

The problem of organic form (e.g., Ritterbush 1968) has two components: design and diversity. Design, or the relationship between form and hypothesized functions, has long been a favored subject of morphologists (Lauder 1982). Russell's discussion of Cuvier reveals the concern of pre-Darwinian morphologists to demonstrate the harmony of form with function in the environment (pp. 33-34). The analysis of design involves in part the discovery of rules that govern the construction of form, and Cuvier laid the foundation of design analysis with his three principles: subordination of characters, correlation of parts, and the functional adaptedness of parts. Russell's treatment of approaches to organismal diversity shows that the unity of plan among organisms was a cornerstone of pre-Darwinian morphology and the basis for the classification and interpretation of diversity. "The aim of this pre-evolutionary morphology had been to discover and work out in detail the unity of plan underlying the diversity of forms, to disentangle the constant in animal form and distinguish from it the accessory and adaptive" (p. 246).

The advent of an evolutionary perspective made little immediate difference to the morphologist's view of the problem of organic form. Ancestry and descent with modification of structure provided a causal basis for unity of plan, but the analysis of design and diversity was little changed. In the 1930s, however, the emerging evolutionary "synthesis" focused the aim of morphological research on the relationship of organisms



to the environment. In the process, the problem of form was redefined. It became less a question of intrinsic relationships and principles of construction (the focus of Cuvier, Owen, and Milne Edwards) and more an issue of explaining form as the product of extrinsic environmental selection.

*Form and Function* ends with the early post-Darwinian era. But the problem of organic form was not resolved. The history of morphology in this century is intimately linked to the rise of the modern evolutionary synthesis and reveals the advent of a transformationist world view that did little to alter the fundamental questions faced by morphologists. What has changed is the context within which problems are debated.

Russell's work subsequent to *Form and Function* was in part a reaction to the mechanistic research program of developmental and evolutionary biology that had increasing prominence after 1900. His later research is important, not for its influence (which was minimal), but for the pattern it reveals in twentieth-century morphology. Russell's objections to the rising "synthetic" view of the evolutionary process were shared by many of his contemporaries, and similar questions have emerged again in the past decade in conjunction with increased criticism of the explanatory power of the modern synthesis.

Four issues have been present throughout twentieth-century morphology. These are the presence of hierarchical systems in biology, the apparent goal directedness of biotic patterns, the antithesis of form and function, and the organism as a historical entity. These four issues are related to the major questions of design and diversity that Russell discussed in *Form and Function*. First, the presence of hierarchical systems in biology. Are there patterns and mechanisms which are not reducible to lower levels? Are organisms hierarchically organized and does this impose constraints on the nature of explanations for organic form? Second, the apparent "directiveness" of biotic patterns. Goal-oriented behavior and directional trends in the fossil record have often been used to justify teleological explanations. What might such patterns say about the mechanisms of structural transformation? Third, the antithesis between form and function. Is the separation real? Can functional and structural patterns be examined independently? Fourth, the organism as a historical entity. Does the past history of



organisms influence the patterns of form and function observed today? To what extent must historical data be incorporated into analyses of form and function, and how can past history be analyzed scientifically?

### Hierarchy

While Russell's view of the organism can be seen as a naively holistic reaction to the growing influence of reductionistic methods in physiology and embryology, a closer analysis reveals a more sophisticated hierarchical approach to organic patterns. Russell recognized levels of organization and explanation in biological systems and his contention was not that physiological and genetic analyses were uninformative. Rather, they provided knowledge of the organism at a level that did not contribute to the study of more integrative behavioral patterns. The philosophy of organism urged by Russell, Agnes Arber, Hans Driesch, J. H. Woodger, and R. S. Lillie recognized relatively little interaction between levels of organization.

In the modern conception, hierarchical systems are decomposable into a set of subsystems or levels, each of which has properties not entirely predictable from an analysis of other levels (Lauder 1981). Hierarchy theory emphasizes: (1) the distinctiveness of patterns and processes at each level, (2) the partial independence of explanation of each level in the hierarchy, and (3) that a general theory must span levels and integrate aspects of each level into a synthetic unit (Simon 1962; Weiss 1971; Whyte et al. 1969). Reductionism and holism differ in the degree to which they conceive of levels as distinct from one another. If the higher levels in an organism, for example, behavior, language, and thought, function with considerable independence from lower level physicochemical processes, then physiological or mechanistic explanations of activity will be unacceptable.


Russell's concept of organism is clearly hierarchical. In his 1924 book, he outlined the three levels he saw as necessary to understand organic activity: conditions for life, functions, and responses (table 1). He insisted that "there is . . . a hierarchy of action extending down from the responses, through the more complex to the simpler functions, and from these to the material conditions, and the explanation of biological phenomena must

## INTRODUCTION

Table 1

E. S. RUSSELL'S

## HIERARCHY OF ORGANIC ACTIVITY

Hierarchical Level	Russell's Examples of Processes within Each Level	Between-Level Analysis (Functional Biology)	Within-Level Analysis
A. Responses	<ol style="list-style-type: none"> <li>1. Self maintenance</li> <li>2. Development</li> <li>3. Reproduction</li> </ol>		Behavior
B. Functions	<ol style="list-style-type: none"> <li>1. Metabolism, feeding digestion, absorption</li> <li>2. Differential growth</li> <li>3. Movement</li> </ol>		General physiology
C. Conditions for Life	<ol style="list-style-type: none"> <li>1. Chemical properties of protoplasm</li> <li>2. Environment required for life</li> <li>3. Chromosome and gene function</li> </ol>		Biophysics, biochemistry

be from above downwards, not, as generally agreed, from below upwards" (1924*b*, p. 111). Therefore, "no single biological function can be fully understood if it is treated merely as a physico-chemical event" (*ibid.*). The aim of Russell's functional biology was "to discover the general laws of response," those acting at the highest level. Each level, he argued, depends on lower levels but cannot be completely reduced to them. He defined responses as "activities manifested by the organism as a whole," and distinguished this level from functions performed by parts of the whole organism. Russell further discriminated response levels by the importance of "psychological activities." The uniqueness of living things, he held, is due to the emergence of an organic mind, which causes an irreducible gap between higher and lower levels. Material determinism failed in not recognizing hierarchical levels. This approach could not possibly explain the emergence of mind in terms of physics and chemistry alone. For Russell, the response level that included perception, striving for goals, flexibility, and need furnished the nucleus of the concept of organism.

Contemporaries of Russell, who rarely cited his work, also addressed the issue of hierarchy in the context of general discussions of the nature of organisms. R. S. Lillie (1945) called the organism a "psychophysical system" and suggested that there was a "vital directiveness" to life. Sounding very much like Russell, he appealed to teleological principles to explain the adaptive and purposive activities of organisms. Lillie believed that natural dissipative and disordering effects would prevent an increase in complexity of structure and function which we know to be a characteristic of living systems: "Observation shows that unguided natural processes tend automatically toward simplicity and uniformity rather than toward complexity and diversity" (Lillie 1945, p. 85). He thought the second law of thermodynamics was the primary factor acting to decrease order; against it natural selection could not prevail to build complex adaptive characters. The botanical morphologist Agnes Arber also advocated a holistic approach to form. She believed that the proper emphasis of morphology was the study of final causation, the essential principle of life that escaped a physicochemical analysis. "It is . . . the business of morphology," she concluded, "to connect into one coherent whole all that may be held to belong to the intrinsic nature of a living being" (Arber 1950).

This concept of an organismic hierarchy certainly was not unique to early twentieth-century morphologists. Cuvier's threefold division of functions into general, animal, and vital and his principles of correlation of parts and subordination of characters clearly indicate a hierarchical approach. Hierarchical analysis is also emerging today in evolutionary morphology as levels of evolutionary patterns and processes above the level of the individual organism are defined (Gould 1980). The intrapopulation level, with its accompanying microevolutionary processes such as change in gene frequency, forms the basal unit of the modern hierarchy, the process of speciation forms the second level, and macroevolutionary patterns and processes form the third level. Empirical investigation reveals hierarchical organization, and the analysis of evolutionary patterns at higher levels increasingly corroborates this concept at the expense of the extrapolationism and transformationism dominant in the modern synthesis of the 1950s and 1960s. Many con-



temporary morphologists are challenging the view that intra-population processes are sufficient to explain patterns exhibited by all monophyletic taxa.

A central tenet of the modern synthesis as it solidified in the 1940s was that gradual allelic substitution over time formed the basis for evolutionary change and for selection resulting in adaptation (Mayr 1963; Simpson 1953; see Gould 1980). The transformationist underpinnings of this model resulted in widespread efforts to ascertain whether mechanisms of speciation and morphological patterns in extant taxa and in the fossil record were consistent with this model of evolutionary change. Arguments from consistency in turn have formed the basis of corroboration for the synthesis as a depiction of the evolutionary process. Stebbins and Ayala (1981) argue that rapid speciation "is not inconsistent with . . . the synthetic theory" and that "large-effect mutations are not incompatible with the synthetic theory."

Many morphologists today hold a hierarchical view of the evolutionary process that stresses both the use of natural evolutionary (monophyletic) lineages and the existence of higher level processes that may act, for example, on the species as a unit (Eldredge 1979). Patterns of speciation, fragmentation of continental areas and their accompanying biotas, and differing rates of evolution in closely related taxa are explained at levels above that of the allele and population. This is not to say that genes do not exert an influence on organismal structure or evolutionary pattern, but rather that processes at the individual or population level are partially decoupled from higher level evolutionary phenomena acting on species and other monophyletic clades.

Gould has suggested that an emerging new and general theory of evolution

will be rooted in a hierarchical view of nature . . . and will possess a common body of causes and constraints, but will recognize that they work in characteristically different ways upon the material of different levels—interdemic change, speciation, and patterns of macroevolution. As its second major departure from current orthodoxy, the new theory will restore to biology a concept of organism. (1980, p. 129)

## Directiveness of Biotic Patterns

The idea that there is an internal mechanism guiding organic change that channels the direction of transformation and gives life its course has a long history in biology (Gould 1977). American paleontologists in the first half of this century were particularly fond of what Gould has called directional-internalist theories of change in which factors intrinsic to the organism drove evolution in certain predetermined directions. H. F. Osborn's *aristogenesis* is one well-known example of a theory that denies the environment a significant role in controlling the direction of change.

Although Russell had remarkably little to say about patterns of structure as exhibited in the fossil record, he held a firmly internalist view of the organism and evolutionary transformation (Russell 1962). Life exhibits directive behavior as a result of its striving to satisfy needs and goals. "Biology must recognize and accept directive activity as an 'irreducible characteristic' of life" (Russell 1945). Such activity is explicable only when the organism is viewed as a whole. As mentioned above, Russell's concepts of drive, direction, and need stem from a theory of hierarchy that views the upper level of organismal response (table 1) as widely separated from lower levels by virtue of the emergence of psychological or "mental" factors in the upper level. Drive and directiveness, in Russell's view, emerged as properties of the hierarchy of organic activity (Russell 1950a) and encompassed individual as well as evolutionary patterns.

Arber, Lillie (1932), and Woodger held generally similar views of directiveness. Lillie summarized his position on this point: "An internal determination, as distinguished from an external or environmental determination, may under appropriate circumstances assume the upper hand and guide the course of vital activity in a manner which is largely independent of environmental conditions" (1945, p. 22).

In its modern formulation, the internalist theme in morphology has two manifestations, both of which avoid the problem of teleology and vitalism, concepts that are never distant in discussions of directive factors in evolution (e.g., Driesch 1914). The first facet of the renewed interest in intrinsic



properties of the organism concerns the role of development in canalizing directions of potential evolutionary change. Not all possible variations on a given body plan are produced with equal frequency. Thus selection acts on nonrandom variations that are a result of interactions between developing parts of the organism and the hierarchical nature of epigenetic programs (Riedl 1978; Zuckerkandl 1976). This means that variation in morphology, as manifested by different patterns of development between individuals of a species, is strongly directional (Alberch 1980). Directional changes emerge as a result of constraints of gene expression and regulation and the conservatism of previous evolutionary ontogenetic patterns. Variation is also biased by the tendency of ancestral epigenetic programs to be maintained in the evolution of organisms. These preserved instructions, then, have the potential of being co-opted for a different purpose at a later time. Riedl's (1978) concept of organism is both internalist and hierarchical in the manner of Russell: both maintain that a systems and integrative view of the organism is necessary to understand evolutionary patterns and that epigenetic interactions may give "internal directionality" to the process of structural transformation (e.g., Russell 1962).

The second part of the revival of internalist approaches consists in the analysis of historical effects and in the determination of the way bodily organization governs structural evolution (Lauder 1981; Whyte 1965). The central question in this analysis is, Are there historical laws of morphological change, that is, general repeatable patterns in the evolution of form and function that stem from intrinsic organizational properties? Directional evolutionary change in morphology may be due to extrinsic environmental pressures as well as the inherited constraints of body plan.

One example of such an intrinsic organizational feature is repetition of structural elements. Repeated components of a structural pattern, such as metameric organization or duplicate genes, provide constructional flexibility by allowing one component of a system to be modified with minimal effect on other elements. The historical effect of repetition of parts is thus structural diversification, and redundant designs may be closely related to evolutionary divergence in form and function.



In *Form and Function*, Russell describes the pre-Darwinian view of the effect that *bauplan* had on morphological diversity. Geoffroy and Owen especially saw unity of plan as the cornerstone of comparative anatomy and the structural basis for the analysis of design. Of Geoffroy, Russell writes, "He holds that the principle of unity of plan and composition is the true base of natural history, and that this unity limits the possible transformations of the organism" (p. 75). Owen also believed that the adaptive expression of form was constrained to vary within limits ordained by the archetype, and he subordinated functional demands to the necessities of structural plan.

### Form and Function

One thread that extends throughout the entire history of morphology is the debate over the primacy of form or function in the analysis of design. Indeed, this antithesis appears to have a universal appeal, evidenced by its recurrence in the analysis of art, literature, and architecture, where explicit analogies with biological designs are often drawn (e.g., Steadman 1979). In a later historical note on form and function, Russell (1936) analyzed two themes in morphology, unity of plan and functional design, and showed how each related to a different position vis à vis the primacy of form or function. Russell's subjects were Cuvier and Geoffroy: "Cuvier's view, then, is that the necessity for functional harmony and ecological adaptation—without which a species could not exist—accounts for the fact that the same types of structure recur, or are repeated . . . for Geoffroy, form determined function." The principle of connections between structural elements was needed to compare different designs.

Although Russell occasionally suggested that the distinction between form and function might be a false one, his sympathies were with Cuvier and Aristotle. Thus, he argued that "structure and function must be treated as one and inseparable," but in advocating a functional or psychobiological view of the organism and by the very choice of categories in the organismal hierarchy (table 1), he seemingly admitted the primacy of function.

The functional method effects a real union between morphology and physiology—the study of form and the study of function—in that it treats the production of form as being a functional activity. It considers form and function together, and never form in isolation from activity. (Russell 1924*b*, p. 134)

Arber saw no antithesis, and in 1950 she summarized her views.

The contrast, which generally is assumed to exist between *form* and *function*, has no reality when the word "form" is given its full content. The treatment of the two conceptions as antithetic has, no doubt, been fostered by the neat alliteration of the phrase, but their assumed opposition is, in the main, traceable to the analogy, mistaken for something approaching an identity, between the works of man, and living beings themselves. (1950, p. 3)

Modern evolutionary morphologists have generally considered form and function to be separate and have often attempted to predict one from the other (but see Dullemeijer 1974 and Bock and von Wahlert 1965 for more holistic perspectives) or have concentrated on one to the exclusion of the other. One recent attempt to relate form to function, developed for the analysis of fossil taxa where function cannot be observed directly, is the paradigm method of Rudwick (1964, 1968). Rudwick's methodology involves four steps. First, a function is proposed for a structure or set of structures. Second, as Rudwick explains, the structural specification is the paradigm for the proposed function: "[The] . . . postulated function must be converted into a structural specification such that, given the properties of the anatomical materials available to the organism concerned, the specification defines the structure that would give optimal efficiency in the performance of that function" (1968, p. 45). Third, the paradigm structural pattern is compared to the actual structures possessed by the organism. Finally, a correlation between the paradigm and the observed structure is taken as evidence that the structure would have been capable of performing the hypothesized function.

Several authors have pointed out potential pitfalls of this method (e.g., Gould 1970; Grant 1972). There is the possibility



of choosing the wrong paradigm and still finding a correspondence with structure; structures may have several functions and thus not fit any one paradigm closely. The constraints imposed by *bauplan* may limit the fit to any particular paradigm. It is impossible using the paradigm method ever to show that a particular structure had no function or was nonadaptive. While Rudwick specifically disavowed any link between structures that conform to a paradigm and the selective value of those structures or reasons for their origin, other authors have used the paradigm concept to demonstrate adaptive and selective value. Gould, for example, proclaimed that "a science of form is now being forged within evolutionary theory. It studies adaptation by quantitative methods, using the organism-machine analogy as a guide." Moreover, mechanical optima (paradigms) are attained by biological structures "because they provide a selective advantage that leads, over and over again, to their attainment in competition" (1970, pp. 77, 110; but see Gould 1980 for a different perspective).

A major goal of evolutionary morphology today is to understand the selective forces that have produced structures (Bock 1980; Cracraft 1981; Gans 1974). In practice, most research in functional morphology follows the general guidelines of the paradigm method, often with the additional stage of inferring selective forces on form and function. Rosen claimed that "selection pressure is the major determinant of structure," that the effect of selection is an optimization of structure, and that phyletic sequences are governed by principles of optimality (1967, p. 68). Thus, when we attempt to explain why a particular structure has evolved, we compare "our actual structure with its optimum expressed in engineer's terms" (Gould 1971, p. 256), an approach rooted in D'Arcy Thompson's contribution to morphology.

The use of optimization models in morphology grew out of the post-Darwinian view that organisms are constrained more by demands of the environment than by *bauplan* and intrinsic organizational features (Gould 1980). Optimality models treat systems at equilibrium and therefore may fail to characterize accurately a system in which intrinsic historical factors have been important determinants of form.



## History

Chapter 17 of *Form and Function* looks at "the organism as a historical being," and assesses the influence of early post-Darwinian transformationism on morphological thought.

We have seen that the coming of evolution made comparatively little difference to pure morphology, that no new criteria of homology were introduced, and that so far as pure morphology was concerned, evolution might still have been conceived as an ideal process precisely as it was by the transcendentalist . . . and it was a point of subordinate importance that, under the influence of evolution-theory, these were considered to represent real ancestral forms rather than purely abstract figments of intelligence (pp. 302-3)

Although descent with modification provided the basis for historical analyses of organismal form in which "present day structure was interpreted in the light of past history," evolutionary morphology "was powerless to bring to fruit the new conception with which evolution-theory had enriched it." Russell approved the historical approach used by O. Hertwig, who showed that placoid scales of sharks and teeth are homologous structures and that dermal bones are often partially formed by the coalescence of tooth rudiments. But he saw the dominant influence of evolution as a rationalization for unbridled "phylogenetic" speculation and the reconstruction of ancestral morphotypes in the manner of pure morphology. Transformationism did not realize its potential to provide a historical basis for the problem of organic form: "To make full use of the conception of the organism as an historical being it is necessary then to understand the causal nexus between ontogeny and phylogeny" (p. 313). This causal connection has received detailed consideration only in the past ten years.

Evolutionary theory as it has been developed and applied under the new synthesis is primarily an equilibrium theory. Organisms and populations are viewed as being in equilibrium with the environment, subject to the influences of their surroundings to such an extent that the analysis of present-day environmental factors alone can be used to understand func-

tional design. The past history of environmental change is not often considered as having an important effect on the current structural pattern, nor is the past sequence of changes in organismal form often believed to effect the patterns of correlation among form, function, and environment (but see Gans 1968).

Evolutionary morphologists must recognize that patterns of structure and function are due not only to the exigencies of the current environment but also to past sequences of phyletic and environmental change. Organisms do retain primitive characters, and design is a compromise between current demand and past history. The principle of historicity (Lewontin 1967) deserves increased attention.

While historical explanations have not been popular for most of the twentieth century (the reasons for this are discussed below), several biologists, Russell among them, did recognize the role of history in molding development and behavior: "The organism is above all a historical being" (Russell 1930, p. 9). Indeed, one of Russell's criticisms of gene theory was that it ignored history, a criticism that has also been applied to modern equilibrium population genetics. Most morphologists in the early twentieth century firmly disputed the value of historical explanation. They argued that it has no power of explanation and that it merely tells us that structures are present today because they were present in ancestral forms. Besides, the study of form had been perverted in the past to serve the end of phylogenetic speculation, and it was time to get on with understanding the causes of form (e.g., Wilson 1901).

This reaction against historical analysis in morphology took two forms. First, experimental embryologists advocated the direct mechanical study of the causes of development and eschewed historical interpretations (Allen 1975; Coleman 1967, 1977). Wilhelm His wrote in his article on the principles of morphology (1888):

Attempts to introduce some elementary physiological or mechanical explanations into embryology have not been generally agreed to by morphologists. To one it seemed ridiculous to speak of the elasticity of the germinal



layers; another thought that by such considerations we put the cart before the horse; and one recent author states that we have something better to do in embryology than to discuss tensions of germinal layers, etc., since all embryological explanation must necessarily be of a phylogenetic nature.

Second, many biologists decried what they perceived to be the unbridled phylogenetic speculation in the period following publication of the *Origin of Species*. Arber was outspoken on this matter:

Morphological and phylogenetic concepts belong to different categories, and only confusion can come of the attempt to reduce these categories to one. (Arber 1937)

The whole attitude of many post-Darwinian botanists . . . has been distorted, through trying to compel the study of form to subserve phylogenetic ends. (Arber 1950, p. 7)

Attempts to introduce phylogenetic interpretations or to use phylogeny as a guide to history lost favor among holistic morphologists. For example, Arber advocated a "pure morphology" with a nonhistorical type concept and complained, "The Darwinian school seized upon Goethe's archetypal flowering plant, and the notion, common to him and de Candolle, of a minor archetype for each family; detached these ideas from their context in the world of thought; set them up in the world of experience; and assumed their actual historic existence (1950, p. 63). D'Arcy Thompson (1917) also largely rejected a historical approach to form, although his coordinate grid transformations can be interpreted as evolutionary changes. Instead he advocated the search for mechanical and physical factors that produce form, thus expressing the equilibrium concept of the organism in its environment that permeates much of evolutionary morphology today: history can be ignored as a component in the explication of organic form.

Garland Allen (1975) has described morphology from 1860 to 1890 as being intimately tied to three research goals: the determination of the unity of plan that underlies the diversity of organic form, the search for archetypal forms (e.g., Haeckel's *Gastrea*), and the reconstruction of phylogenetic trees. The first



two aims had a strong pre-Darwinian heritage. Allen saw a "revolt from morphology" beginning in 1890, that had its origins in the "Berlin group" physiology of the 1840s and that was manifested by the rising interest in *Entwicklungsmechanik* as fostered by Roux and His. The experimental method and explicit hypothesis testing were well-known objectives of this approach.

The rise of experimentalism was accompanied by a rejection of many of the explanatory paradigms used by descriptive morphologists in the late nineteenth century (Coleman 1977; Roll-Hansen 1976). Gegenbaur and Haeckel saw history as an explanation and felt that the past sequence of change in form or ontogenetic pathways in character development did have explanatory content (Haeckel 1874). But descriptive morphology did not cease with the rise of experimental embryology. Arber, Hyatt, Marsh, Russell, Portmann (e.g., 1948), Naef (1919; see Zangerl 1948), Cope, and D'Arcy Thompson certainly had a considerable interest in organic form. Morphology as the study of form was not itself the subject of a "revolt." The significant change near the turn of the century occurred with new views of the nature of acceptable explanations for form. History was not a component of morphological explanation, and this was as true for many morphologists (Arber and D'Arcy Thompson) as it was for experimentalists (Roux, His, T. H. Morgan). And as the modern synthesis began to take form in the 1920s, it too, by its emphasis on the environment, equilibrium, and extrinsic explanations shared the nonhistorical methodology common to experimental embryology and holistic morphology.

If any one feature has been characteristic of evolutionary biology in the last decade, it is renewed interest in the theory and practice of phylogenetic systematics and in the accompanying historical interpretations. Historical biology is emerging as a discipline with a distinct methodology and aim: the analysis of patterns of organismal form, function, and distribution through time based on patterns of phylogenetic relationship (Eldredge and Cracraft 1980; Lauder 1982; Nelson and Platnick 1981; Wiley 1981).

Three principles underlie recent methods of historical analysis. (1) Organisms may be ordered into nested sets based

on an analysis of uniquely derived features, and transformation series, homologies, and convergences are recognized a posteriori on the basis of character distributions. (2) These nested sets of taxa may be interpreted as a phylogeny, reflecting genealogical relationships between clades. (3) The phylogenetic pattern of relationships and the distribution of structural features specified by accepting any particular phylogeny may be used as a basis for interpreting functional and geographic patterns.

Central to this emerging historical biology is the distinction between evolutionary patterns and processes (Eldredge and Cracraft 1980) and the explicit testing of theories of process by their predicted patterns. Historical explanations, in order to be testable, must involve general, not unique, features of organisms and must apply to classes of monophyletic taxa. The "new morphology" (Coleman 1980, p. 179) thus is not based on a search for mechanisms and is not firmly rooted in the modern synthesis. Morphological investigation increasingly emphasizes historical patterns and explanations and questions the testability of many theories of process.

#### MORPHOLOGY: DECLINE AND RENAISSANCE IN THE TWENTIETH CENTURY

Morphology was a discipline in full flower when the *Origin of Species* appeared. Cuvier, Louis Agassiz, and Owen were primarily responsible both for the considerable popularity of comparative morphology as a branch of natural philosophy and for the elucidation of two fundamental concepts: design and diversity. Early post-Darwinian morphologists inherited "a fully formed morphology with set and definite principles" (p. 246). These principles included the use of topological correspondence in reconstructing archetypes (Geoffroy's principle of connections) and the principle of correlation of parts for understanding design. The diversity of organic form was the subject of increasingly detailed analysis as unity of plan was revealed in many small features of anatomical construction.

In this century, the discipline of morphology has lost the eminent position it had in the last. Gegenbaur, Haeckel, Lankester, Goodrich, and others (see *Form and Function*



chapter 14) were unable to broaden the conceptual foundations of morphology, and the study of comparative anatomy declined with the rise of the modern evolutionary synthesis. Russell and other holistic morphologists attempted to counter this decline by emphasizing form and structure in opposition to mechanism and environment, but their efforts were in vain. These individuals became increasingly isolated from the mainstream of biological research after 1920.

The discipline of morphology contributed little to the emerging synthetic evolutionary biology of the 1930s. Ghiselin has attributed this to the nature of morphological investigation (itself a reflection of the esteem of morphology among many neo-Darwinians).

Morphology has contributed so little primarily because it has had so little to contribute. It is a descriptive science of form, and only when conjoined with other disciplines does it tell us anything about causes. But once a causal mechanism has been accepted, it can provide a valuable service. Nonetheless, for this very reason, morphology tends to be the sort of discipline that will follow, rather than lead, in the development of evolutionary theory. (1980, p. 181)

Mayr proclaimed, "Comparative anatomy more or less stagnated after the promising start in Darwin's lifetime" (1980a, p. 173). The reasons for this may have less to do with any inherent deficiency in the nature of morphological research, as suggested by Ghiselin, than with the nature of the modern synthesis as a nonhistorical, equilibrium program. After all, morphology hardly was undistinguished in the time of Cuvier, Agassiz, and Owen, when the two great morphological concepts, unity of plan (diversity) and functional design, were active topics of research. Indeed, it was the queen of the biological sciences. Why was morphology so completely eclipsed by mechanistic research in the early twentieth century?

Four features of the hardening evolutionary orthodoxy from 1940 to 1965 had a negative impact on theoretical research in form and function. Consider first the synthesist's argument from consistency. A key aspect of the emerging synthesis was the attempt to bring morphological patterns, macroevolution,



and speciation under the umbrella of genetics by showing that these patterns are consistent with genetic theory (Mayr 1980b, p. 1). The use of consistency as a criterion for evaluating the theory of evolution continues to the present day (Stebbins and Ayala 1981). This form of explanation, however, makes falsification of the theory difficult if not impossible, for nearly any new observation can be interpreted as being consistent. Where were the predictions that morphologists could test to see whether major structural patterns (as revealed by paleontology, systematics, and comparative morphology) corroborated or refuted hypotheses based on the evolutionary synthesis? There were none. As a result, the best investigators (e.g., Goodrich, Romer) either continued to produce comparative anatomical treatises which "could have been written, had the factual material been available, by Gegenbaur or virtually any other late nineteenth-century morphologist" (Coleman 1980, pp. 175-76), or abandoned the mechanistic research program altogether in favor of holism (Arber and Russell). Given the dearth of testable evolutionary hypotheses, many morphologists devoted themselves to discovering consistencies between their data and the conceptual framework provided by the emerging synthesis.

A second feature of the incipient evolutionary paradigm was equilibrium methodology and its emphasis on extrinsic factors as the dominant influence on form. Neo-Darwinism effected a subtle change in our view of the organism that is only now being reconsidered. Instead of looking at organisms as products of history with intrinsic factors, constraints of phylogeny, and structural and functional design, as important and valid subjects for research (the province of morphology), neo-Darwinian views focused on the relationship between the organism and the environment. Adaptation, environmental "forces" on the organism, and competition became the major features of the evolutionary research program. Ecology took precedence over morphology (Ghiselin 1974). In this regard, it is true today that the primary neo-Darwinian interest in form lies in its manifestation of environmental influence. The field of biomechanics is concerned largely with the responses (both structural and functional) of organisms to forces exerted by the environment. What are the limits to biological design imposed by extrinsic factors (Wainwright 1975, 1980), and what are the

mechanical principles used in constructing biological systems? The premise underlying most ecological and functional research is that an equilibrium exists between the organism and the environment and that the environmental forces observable today are those that have influenced form in the recent past. The themes of hierarchy and intrinsic structural organization have not, until recently, been prominent in modern morphology. Changing selection forces through time and patterns of covariation between structure and environment have instead been supported as the primary determinants of morphological change.

The third component of the modern synthesis that affected morphology was the focus on mechanisms and on theories of process. Pre-Darwinian morphology emphasized the study of pattern, not the process of transformation, and was concerned with elucidating structural principles of design. Louis Agassiz summed up his life's work with a statement about structural patterns: "I have shown that there is a correspondence between the succession of forms in geological times and the different stages of their growth in the egg—this is all" (cited in Wilson 1901). But the rising tide of mechanistic research on two fronts, natural selection and the environment as the mechanism of transmutation of form and experimental methods in developmental morphology, provoked two responses from morphologists. One, holism, is represented by Arber, Russell, Grassé, and to some extent Portmann (1952), among others. The second response consisted of trying to fit morphological research into a mechanistic framework. Morphologists searched for explanations of structure in terms of selection, adaptation, and environmental forces even though these processes were rarely demonstrated. The morphological tradition within the evolutionary synthesis is dominated by the axiomatic use of process concepts. This is largely due to an error in interpreting hierarchical level. Most morphological research consisted of comparisons between individuals in different genera, families, or orders. Selective forces on form were hypothesized by examining large-scale differences in form and proposing environmental factors that could account for them. Analysis at this general level was assumed to provide insight into selective processes acting at the lower level of individuals within a species. Research in evolutionary morphology rarely focused



on intrapopulation variability and comparisons between closely related species, the level needed if information about selection and adaptation is to be obtained.

The loss of the concept of hierarchy is the fourth aspect of the evolutionary synthesis that negatively affected research in morphology. With the advent of Darwinian theory and its emphasis on adaptation, the environment, and the continuity of natural evolutionary units through time, the transformation of form became a key focus of morphological research (Eldredge 1979). How do structures and functions change through time as a result of the environment? How might organisms be arranged into ancestral and descendent sequences? What types of intermediate designs need to be postulated in order to construct a smooth evolutionary transformation or series of forms between two distinct extant types? As a consequence of the emphasis on continuity through time, discrete evolutionary units such as species were denied separate ontological status (Eldredge 1979). A transformational or extrapolationist approach (Gould 1980), reducing the problem of form to one solely of genetic change, became part and parcel of the evolutionary synthesis.

Morphological research was not immune from transformationism. The construction of morphological series became an important research procedure in both the reconstruction of phylogenies and analyses of the evolutionary modification of structure and function (Lauder 1981). These series of forms, usually ordered without regard to genealogical relationship, represent a hypothesized transformational pathway that was used to infer selection pressures, evolutionary trends, and changes in adaptive zone.

The evolutionary synthesis, through the transformational, equilibrium, and inductive character of the research program it fostered, shifted the focus of morphological research away from its pre-Darwinian emphasis on principles of structural organization. The new aim became the demonstration that morphological data were consistent with the synthesis and the axiomatic (not deductive) use of neo-Darwinian process concepts. If these efforts resulted in the failure of morphology to contribute to the evolutionary synthesis, it is perhaps because arguments of consistency and the constant interpretation of

data in light of another theory are unlikely to lead to new theoretical advances, rather than because of any inherent deficiency in morphological data or concepts.

In many ways modern morphology is returning to its pre-Darwinian focus on structural patterns and principles of organismal design and is emerging from its post-Darwinian decline. There is renewed interest in the intrinsic structural organization of organic systems and the influence that properties such as complexity and redundancy have on the evolutionary transformation of design. Russell's *Form and Function* is important because it demonstrates the persistent nature of the problems faced by those who study organic form. The modern synthesis reduced the problem of form to one of genes and environments. Now morphologists are returning to the study of structure within a historical and hierarchical framework and are attempting again to understand design and diversity.

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