# Nature's Purposes

## Analyses of Function and Design in Biology

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# Introduction

Biology is unique among the natural sciences in licensing apparently teleological statements about design, purpose, and adaptive function. Teleological thinking originated from two views, both of which are assumed to have been discredited in physics, chemistry, and the other natural sciences. The first source of teleological ideas is the Aristotelian view (discredited by Galileo) that the motions of natural objects are explained by their possessing intrinsic purposes that are fulfilled so long as the objects are not subject to external interference. The second source, abandoned by scientists as untestable and irrelevant to scientific explanation, is the view that every phenomenon in the natural world is an instance of the direct operation of divine will. Modern biologists also cleave to the unsuitability of such Aristotelian and theistical underpinnings for teleological claims.

Nonetheless, teleology has seemed to many theorists to be indispensable to biology. To understand the complex morphological and behavioral traits of organisms it seems we must say what those traits are for, which is to give a teleological explanation of why organisms have them. Other biologists have argued that natural selection, providing, at root, statistical explanations for why organisms have the traits they do, obviates any need for teleological thinking (Dawkins 1987). If organisms possess structures that can be explained fully as having arisen by selection on randomly (in the sense of "undirected") originating variants, then what need is there for teleology, a designer, or indeed even the notion of design (Dawkins 1996)? There is an evident and uncomfortable tension within the biological sciences over the role that teleological explanations might play. Furthermore, if teleology cannot be eliminated from biology, this raises fundamental questions about the nature of biological explanation and the relationship of biology to the rest of science.

Because the account we give of the role of teleology in biology will have consequences for our conception of the nature of biology itself, the goal of accounting for "Nature's purposes" is arguably the most important foundational issue in the philosophy of biology. Given the significance of the topic, it is unsurprising that many essays by biologists and philosophers of biology have been attempts to come to terms with teleology. And although most good anthologies in the philosophy of biology include a sample of this literature (e.g., Sober 1994), no comprehensive collections have previously been available. (Rescher [1986] provides an anthology derived from conference proceedings and Buller [1998] presents an anthology that focuses on philosophical literature.) Why this should be so, when the other major topics in the philosophy of biology have been anthologized several times over, remains curious. That we have the temerity to attempt to fill this breach is perhaps partly explained by the fact that as a philosopher, an ethologist, and a comparative morphologist, each of us can feel confident enough to blame the others if our readers detect any glaring omissions. On the positive side, our different backgrounds have, we believe, allowed us to bring together different parts of the interdisciplinary literature on biological teleology. Philosophers, for instance, seem to have been largely unaware of the literature on teleology generated by workers in functional and evolutionary morphology, and we hope to have closed gaps that exist even among biologists themselves.

Our selections for this volume have been chosen to reflect attempts to understand biological teleology from within a *naturalistic* framework. Following Darwin, rather than interpreting claims about design and function in biological systems as literal or metaphorical references to the supernatural intentions and interventions of a Cosmic Designer, most modern commentators interpret teleological claims to be referring more or less circuitously to various natural processes or properties. There is disagreement at many levels over the merits of the various theories offered, but it is possible to identify a number of central themes (Allen and Bekoff 1995). At the most basic level is a dispute about the point of making teleological claims: Does attributing the function of pumping blood to a heart *explain* anything, or is it merely a shorthand description of certain attributes of the heart? Most of the selections in this anthology maintain that teleological claims in biology both describe and explain something, although opinions vary about exactly what is explained, and how. (For a defense of the view that teleological claims are merely descriptive, see Thompson 1987 and Lipton and Thompson 1988a, b.) Some authors maintain that teleological explanations are a species of causal explanation. Others argue that teleological claims apply to biological phenomena independently of any particular causal explanation, and that teleological claims are best understood as providing a framework for causal explanation.

Among those who accept some version of the claim that the point of making teleological claims is to give or to frame explanations, there is disagreement about what exactly is explained by teleological claims. Here the major division is between, on the one hand, the view that teleological claims correspond to explanations of the presence or maintenance of particular traits of organisms (e.g., the fact that hearts pump blood helps explain why organisms have hearts) and, on the other hand, the view that teleological claims explain how a particular component of a system contributes to some other capacity (e.g., the fact that hearts pump blood helps explain how organisms do a variety of things, such as getting oxygen to their tissues or locomotion). Our selections reveal considerable sympathy for both of these views, and some of our authors attempt to show how the two views may be combined in various ways.

Those who focus on explanation of the existence of traits are divided on the question of whether natural selection should feature in an account of the use of teleological language in biology. Should theorists be attempting to give a *conceptual analysis* of teleological notions that have roots prior to Darwin and outside biology, or are they free to cut ties to past uses of teleological language and to promote a new understanding of such language on grounds of its utility within Darwin's theory? A classic example of the use of teleological language in biology is William Harvey's seventeenth century claim that a function of the heart is to pump blood. If Harvey could know what hearts were for without knowing anything about Darwin's theory, then why does the proper analysis of Harvey's claim need to make any reference to the theory of evolution? And if natural selection is a key part of the understanding of teleological language in biology, should teleological explanations be understood in terms of the history of selection that has produced particular traits, or should it be understood in terms of the disposition of these traits to contribute to the future survival and reproduction of organisms subject to natural selection? The choice between these backward-looking and forward-looking alternatives is a theme of several of the papers in our selection.

We have attempted to order the articles in this anthology so that readers who are new to the topic of biological teleology are offered the best chance of being able to read and understand this literature. Because themes tend to cluster, a strictly historical ordering is not the best. But because later papers often presuppose some knowledge of the earlier literature, it is not appropriate to organize them entirely on thematic grounds. Thus we have attempted to compromise. First we present some of the early papers that address the role of past events of natural selection in grounding teleological claims. Then we present some of the early papers that present alternatives to these backward-looking views. The remainder of the selections represent various attempts to become more sophisticated about the goals of philosophical analysis, and the variety of uses of teleological language that is found in actual biological practice. We believe the anthology is suitable for an advanced undergraduate or graduate course.

## Looking Backwards: Teleology as Etiology

Given the centrality of Darwin's theory of evolution in modern biology, many authors have attempted to explain the role of teleology within biology by invoking natural selection. We begin with such an account from biologist Francisco J. Ayala. Teleological explanations in biology are justified, according to Ayala, in three kinds of cases: (i) when an end-state or goal is consciously anticipated by the agent, (ii) in connection with self-regulating systems (e.g. regulation of body temperature), and (iii) in reference to structures anatomically and physiologically designed by natural selection to perform a certain function. Ultimately, Ayala believes, the first two kinds of cases are grounded in the third—design by natural selection, which is an undirected, historical process. Ayala's account of teleology is, therefore, historical (or "backward-looking"). He argues that because natural selection is a mechanistic process, the teleology found in biology is "internal"—there is no need for an external source of purpose or design in the form of a Creator—and it is devoid of any suggestion that there are preordained goals.

Among biologists, the term *teleology* is ambiguous. Some authors use it to refer only to those cases involving preordained goals (either Aristotelian internal purposes, or theistical external purposes) while others employ it generically for all uses of the notions of function, design, or adaptation. Ayala says that he would be happy to see the term restricted to cases involving preordination, and even eliminated from science altogether. But rather than haggle over terminology, it is important, he thinks, to clarify the various ways in which the term is used, and he rejects the suggestion (e.g., Mayr 1965; Pittendrigh 1958) that biologists would do better to abandon the term *teleology* and use *teleonomy* only in cases of end-directed systems with self-regulating mechanisms ("programs" in the jargon of Mayr 1988). Ayala points out that some biological phenomena are end-directed without being self-regulating.

Ayala also raises the important issue of the nature of teleological *explanation*. He explains and accepts Ernest Nagel's (1965) argument that teleological explanations may be reformulated as nonteleological, causal-mechanistic explanations. Despite this, he argues, teleological explanations are indispensable to biology because they connote that biological systems are "directively organized" whereas nonteleological explanations carry no such connotations; furthermore, teleological explanations are specifically directed at explaining the *existence* of the features of organisms.

Ayala's claim that the target of teleological explanation is the existence of biological traits is taken up in more detail by philosopher Larry Wright. Unlike Ayala, and perhaps because he comes to the topic as a philosopher and not a biologist, Wright is concerned not to prejudge any questions about the relationship between teleological language in biology and its use in other contexts. He chooses to focus on the notion of *function*, and the outcome of his investigations is, he maintains, an analysis of function that is not restricted to *biological* functions. According to his analysis (p. 71), *the function of* X *is* Z means:

a. X is there because it does Z, and
b. Z is a consequence (or result) of X's being there.

Although this schema makes no reference to natural selection, natural selection is held to satisfy it, because selected traits are present in offspring given the consequences those traits had for the fitness of parents. Like Ayala, Wright maintains that teleological explanations are explanations of the existence of some state of affairs. Teleological explanation is a species of causal explanation, following the first clause of his analysis, but is distinguished from standard causal explanations by what he calls the "convolution" of the second clause.

Although Wright does not explicitly distinguish between trait tokens (or instances) and trait types, it is important to do so in order to make sense of his claim that his analysis fits a causal pattern. The presence of a token or instance of a trait cannot be causally explained by any direct effect of that instance, for the token's existence must predate its performance of any function. (Millikan, chapter 10, asserts that this is exactly what Wright's analysis commits him to, but Nagel, chapter 7, attributes something like the token-type distinction to Wright.) If the token-type distinction is applied, then a functional explanation can provide the "causal background" for the presence of some feature or trait through the history of traits of the same type performing the effect now designated as a function. In this way, Wright's analysis, like Ayala's, is backward-looking. Because of his use of the term *etiology*, Wright's and other backward-looking accounts of function have come to be known as *etiological* accounts within the philosophical literature.

In our third selection, philosopher Robert Brandon is critical of attempts (such as Wright's) to provide an account of teleological explanation that is not tied to any particular biological theory. Nonetheless, he accepts an account of teleological explanation in biology that, like Wright's, is backward-looking. But unlike Wright, Brandon focuses on adaptations rather than functions. Indeed, borrowing a distinction from Mayr (1961), Brandon separates functional from evolutionary questions: *functional biology* is concerned with questions about how structural elements interact, whereas *evolutionary biology* is concerned with *why* an organism has a particular trait, or *what* the trait is *for*. This use of the term *function* presents a potential for terminological confusion, as several authors use it in the context of evolutionary kinds of questions.

Brandon claims that the proper objects of what-for questions are adaptations: phenotypic traits that have evolved as a direct product of natural selection. Given that a particular trait *A* is an adaptation, the structure of a teleological explanation is that (p. 92) "trait *A*'s existence is explained in terms of effects of past instances of *A*; but not just any effects: we cite only those effects relevant to the adaptedness of possessors of *A*." The notion of adaptation is teleological, according to Brandon, precisely because it is used to answer what-for questions—a form of question that does not arise in the other natural sciences.

Many biologists are concerned that appeals to the past undermine their ability to apply teleological concepts rigorously. Especially in the case of fossils, it is extremely difficult to reconstruct the conditions in which organisms lived, and hence extremely difficult to assess claims about natural selection in the past. Brandon comments (p. 91) that the epistemological problems of assessments about past natural selection "simply show that evolutionary biology is far from being completed as a science." But many biologists would find this too cavalier. Nowhere are the problems more acute than for comparative morphologists working on fossils, and it is therefore unsurprising that they have often taken an entirely different approach to the notion of function, as several selections below will illustrate. Some philosophers, too, have rejected etiological accounts, and the papers in the next section cover some of the major alternatives.

## Don't Look Back: Nonhistorical Approaches to Biological Teleology

We begin this section with morphologist Martin Rudwick's attempt to deal with the particular difficulties of attributing functions to the traits of fossilized organisms. Teleological language, he argues, is appropriate to organisms in just the same sense that it is appropriate to machines whose "*design* enables them to *function* for their intended *purpose*," which, in the case of organisms, is "the existence and survival of the individual organism" (p. 108). According to Rudwick, the inference of function from fossils is driven by our comprehension of engineering principles that constrain the possible roles that some structure might play in the life of an organism. While similarities to existing organisms may provide initial clues, Rudwick maintains that hypotheses about function must be tested by analyses of the sort provided by mechanical engineering. Rudwick maintains that this kind of functional analysis is "logically independent of the origin of the structures concerned.... thus logically unrelated to any and all evolutionary theories." Despite this, he argues, evolutionary theory, insofar as it stresses the adapted, machine-like character of organisms, encourages the attribution of function to fossilized forms. Rudwick's analysis of function is entirely ahistorical, for the properties revealed by an engineering-style analysis of a given structure are properties that it has presently and independently of the context in which the structure might have been used by an organism.

Like Rudwick, morphologists Walter Bock and Gerd von Wahlert are motivated to define *function* without reference to history. They claim that biologists have tended to use the term in two senses, both for what a structure is capable of based on its physical and chemical properties, and for its role in the life of the organism. Bock and von Wahlert suggest that function should be used only in the first sense. More precisely, they define a feature's functions as "all physical and chemical properties arising from its form ... that ... do not mention any reference to the environment of the organism" (p. 124). Function is distinguished sharply from *biological role*, "which includes all actions or uses of the ... feature by the organism in the course of its life history ... with reference to the environment of the organism" (p. 131). These definitions are intended to reform biological practice so as to eliminate the ambiguity inherent in using *function* in two senses, even though restricting function to the first sense "may seem initially strange and awkward to many biologists" (p. 126). The consequence of this reform would be, they believe, a notion of function "free ... of any form of teleology, Aristotelian or otherwise" (p. 125).

The benefit of distinguishing function from biological role lies, according to Bock and von Wahlert, in the clearer picture of biological adaptation that results. Understanding functions independently of and prior to

biological role clarifies, they believe, the way in which features of organisms come to have a biological role within specific environments. Bock and von Wahlert believe that backward-looking approaches may in fact hinder understanding of the principles of evolutionary change, and they claim that (p. 162) "all evolutionary mechanisms can be studied best by working forward through time and without the aid of hindsight."

Working independently, philosopher Robert Cummins produces an account of function that shares some affinities with but also has significant differences from morphologists' attempts to come to terms with functions. Cummins' view is that the functions of a trait of an organism must be specified relative to a "capacity"—a trait's functions with respect to a capacity are those effects of the trait that help to explain how the organism has a particular capacity. For instance, functions of a pigeon's wings with respect to the pigeon's capacity for flight are to generate lift and propulsion, for this explains how the wings contribute to flight. Cummins' description of *functional analysis* can be seen as a precise statement of Rudwick's idea that function attributions are those that would be provided by an engineering analysis. Like the morphologists' accounts, Cummins' is entirely ahistorical. They also share the consequence that anything that has a function must presently be capable of carrying out that function. (This is controversial among the philosophers who defend the etiological account.) The similarities between Cummins' account and those of the previous two chapters should not be pushed too hard, however. There is no restriction on Cummins' part to properties of traits that make no reference to the environment—indeed, quite the opposite is the case, for most capacities will be specified in relation to environments.

Cummins is also concerned with broader issues in the philosophy of biology. In particular, he rejects the attempts by some philosophers (e.g., Nagel 1961 and Hempel 1965) to show that there is nothing distinctive about functional explanations in biology by assimilating such explanations to patterns of explanations found in the other natural sciences. According to Cummins, previous attempts to understand the notion of function have been misled by a pair of assumptions. One of these is the assumption that functional explanations are of the *presence* of a trait. This, Cummins thinks, misrepresents the character of evolutionary theory, according to which traits do not originate because of their functions, but rather are due to factors such as random genetic mutation. The other assumption is that the performance of a biological function by a trait increases the fitness of the organism that has that trait. Cummins suggests that a counterexample to this assumption is the fact that we would call the enablement of flight a function of pigeon's wings even if circumstances had changed so that flying no longer made a positive contribution to the survival and reproduction of pigeons. By making all functional claims explicitly relative to the analysis of a larger capacity, Cummins can explain, for example, why wings would still have the function of enabling flight under the circumstances where flight was no longer to the advantage of pigeons—because they feature in an analysis of the pigeon's capacity to fly.

The views of philosopher Ernest Nagel provide a backdrop to the arguments of several of the papers in this anthology, but we have chosen to include a 1977 paper of Nagel's for inclusion in this volume. We include this paper at this point because, as the title "Teleology Revisited" suggests, it represents a return to address various challenges presented to Nagel's earlier work. There is a wealth of material in the paper that is too great to summarize here, but one of the main features is a careful discussion of the distinction between function and goal-directedness. Nagel criticizes Mayr's conflation of being controlled by a program with being goal-directed, pointing out that being controlled by a program does not entail having a goal. (This is the flip of Ayala's point that having a goal or end does not entail having a program.)

Nagel's view is that functional statements in biology are equivalent to statements without functional terms. For example, he claims that "The function of chlorophyll in plants is to enable plants to perform photosynthesis" is equivalent to "When a plant is provided with water, carbon dioxide, and sunlight, it manufactures starch only if the plant contains chlorophyll." Nagel canvasses various alternative views about function, including those of Cummins, Wright, and Bock and von Wahlert. A major disagreement with Wright concerns Nagel's denial that functional explanations are causal explanations. Nagel contends that while *goal-ascribing* explanations are causal explanations, *functional* explanations are not, because the function of a particular trait does not account causally for the presence of that trait. Rather (p. 238), "explanations of function ascriptions make evident one role some item plays in a given system." But this is to concentrate on an effect rather than a cause—photosynthesis is an effect, not the cause, of chlorophyll.

Nagel's insistence on regarding functions as effects prefigures the forward-looking account of function provided by John Bigelow and Robert Pargetter. "In describing the function of some biological character," they begin, "we describe some presently existing item by reference to some future event or state of affairs." Thus, Bigelow and Pargetter signal explicitly their rejection of backward-looking, etiological analyses of function. After rejecting the idea that functional talk can be eliminated from biology, they strive to show how a forward-looking account of function can be explanatorily relevant yet remain faithful to the principle that there is no such thing as backward causation. They charge that etiological theories, are, in fact, explanatorily vacuous, for if functions are defined in terms of effects that cause the proliferation of traits with those functions, then it is circular to explain the presence of those traits in terms of those functions. Bigelow and Pargetter proffer an account of functions that likens them to propensities: a function of a trait is some effect of the trait that has the propensity to confer a survival advantage to the organism possessing the trait. In this way, functional explanations in biology are likened to those in other sciences that cite propensities to explain certain events (such as the propensity of sugar to dissolve in water).

An entirely different approach to function is provided by philosopher Mark Bedau, who argues that all of the standard naturalizing accounts of teleological language have a common feature: they replace the evaluative component of teleology—what things are *good* for—with a descriptive, value-neutral approach. This, Bedau thinks, is a mistake, and after criticizing the various major accounts, he distinguishes three grades of involvement for value in teleology, ranging from the mere (and possibly accidental) production of good effects (level 1), through selection on the basis of effects that are good, but not necessarily *because* they are good (level 2), to the causal role played by a "telic mechanism," such as the conscious anticipation of good effects, which selects things because they are good (level 3). Bedau argues that biological teleology does not exemplify the highest grade of teleology: natural selection only accidentally selects the things that are good for organisms, for example, swimming is good for fish, and fins were selected for in fish because they contribute to swimming, but fins were not selected *because* swimming is good. (In Sober's [1984] terminology one can say that there is selection *of* things that are good for organisms, but not selection *for* things that are good.) In Bedau's terms, biological teleology is only second-grade teleology, and it remains controversial insofar as we fail to distinguish carefully between the second and third grades. Bedau believes that bringing the notion of value to center stage is compatible with a naturalistic view of biological teleology, wherein "values would be real ineliminable natural properties, subject to broadly scientific investigation" (Bedau 1991, p. 655). The naturalness of value properties remains an important and unresolved issue in ethical theory (Sayre-McCord 1998), and although we think it unlikely that Bedau's position will hold much immediate appeal for practicing biologists (see Allen and Bekoff 1995), we also believe that it is important to keep all options in view.

## Critical Developments

In this section we present a selection of papers that criticize, develop, and extend the positions introduced so far. Several of these papers are also much more explicit about the methodology of providing accounts of teleological functions.

We begin with philosopher Ruth Millikan's defense of an account of function that is explicitly wedded to natural selection. In her 1984 book *Language, Thought, and Other Biological Categories*, Millikan constructed a theory of what she called "proper" functions that was intended to support a theory of linguistic and psychological meaning in terms of the biological functions of language and thought. Many commentators have characterized Millikan's view as a more sophisticated version of Wright's, although in the paper included here she denies that there is any overlap between her theory and Wright's (see her footnote 5). Whatever the merits of likening Millikan's account of function to Wright's, her theory is backward-looking, and it is not necessarily restricted to biological function. Her account, however, specifies much more completely than any previous theory the structural requirements for the existence of a function. This is done in a way that is intended to correspond to the structure of Darwin's theory. These details far exceed any of those presented so far—as she say, it "consumes two chapters" of the earlier book. In the present paper she merely sketches her account before proceeding to her main objectives, which are to contrast her account with others that have been offered, and to take a more reflective look at the objectives of providing an account of function.

A central point of Millikan's paper is to dispute the idea that the philosophical project of characterizing function is one of *conceptual analysis*: the project of finding necessary and sufficient conditions for the application of terms according to (intuitions about) preestablished usage. She argues that the definition of proper function that she provides is intended instead as a *theoretical definition*, to be accepted or rejected insofar as it is part of a successful theory of biological phenomena. Seen in this way, Millikan believes, the philosopher's practice of constructing fanciful hypothetical cases to test intuitions about the applicability of definitions is of rather limited usefulness. One example that has been used frequently to challenge etiological accounts of function is that of a "structural double" (this term is from Mitchell, chapter 14; see also Neander, chapter 11)—a creature that, for instance, is indistinguishable from a human being but comes into existence by an unusual route, such as a massive coincidence of quantum effects. Many philosophers have the intuition that such a creature would have a heart whose function it is to pump blood (and Cummins' account can explain this intuition) but Millikan rejects examples of complex creatures created ex nihilo (and hence, on her account, without function) as irrelevant to the project of understanding the role that functions play in actual biological systems.

Millikan argues for the superiority of her theory over non-etiological accounts given its ability to provide the correct account of things that fail to perform their functions. She believes that alternative accounts of function, such as Cummins', yield the wrong theoretical results, for they imply (as Cummins indeed explicitly noted) that anything that has a function must be capable of carrying out that function. But as Millikan points out, it can be the function of a diseased heart to pump blood even if it is utterly incapable of doing so. The backward-looking theory of function can explain this because it is the pumping of blood by ancestral hearts that accounts, via natural selection, for the function of the present organ no matter how deformed

We have also included a paper by philosopher Karen Neander, who espouses an etiological account of function but disagrees with Millikan's claim that the philosopher's task is more like theoretical definition than conceptual analysis. On Neander's view theoretical definition and conceptual analysis are interdependent, particularly when it is scientific concepts that are being analyzed. Neander then proceeds to respond to three objections commonly raised against etiological accounts of function. The first involves Harvey's attributions of function to hearts in the absence of any knowledge of natural selection. Neander's response is that it is possible to identify things correctly, even if the basis for the identification is faulty. The second objection is that even if Darwin's theory is false, there would still be proper functions, so it is incorrect to define functions in terms of Darwinian theory. Neander's response to this objection is that if the theory of evolution by natural selection is false, this would show only that the definition is false, but it would not show that the etiological account is an incorrect analysis of biologists' current concept of function. The third objection is that of the possibility of creatures, or traits of creatures, that do not have a standard biological ancestry. Millikan rejected such examples on the grounds that they were irrelevant to theoretical definitions of function, but this option is not available to Neander because she accepts the goals of conceptual analysis. Instead, she argues against the intuition that functions could be attributed in the absence of historical knowledge. Even if the argument at the level of intuitions is not convincing, Neander believes that a direct attack on ahistorical accounts of function can be mounted. Like Millikan, she argues that none of the alternatives can account for the *normativity* of function, including the fact that biological structures are *supposed* to perform certain functions whether or not they are capable of performing that function.

Philosopher Ron Amundson and morphologist George Lauder contest what they see as the encroaching orthodoxy that etiological accounts of function are uniquely appropriate to evolutionary biology. Rather, they argue, a Cummins-style analysis should be preferred for the purposes of comparative and functional anatomy. They believe that etiological

accounts place biologists in an untenable position because of the empirical difficulties involved in establishing the historical facts said to underlie function attributions. Amundson and Lauder defend Cummins' notion of function against the criticisms made by Millikan, Neander, and others. In particular, they maintain that the etiologists' criticisms of Cummins' view are based on unequal treatment of the rival accounts of function with respect to their application to ordinary, nonscientific statements about function. Amundson and Lauder detail the ways in which organismic traits are in fact identified morphologically rather than functionally, thus arguing against the claim that the identification of traits in terms of their historical function is essential to biological practice.

Philosophers Berent Enç and Fred Adams, in the next paper, compare etiological with forward-looking accounts of biological teleology and conclude that while etiological accounts have the upper hand on issues relating to the attribution of function, there is nothing to choose between the two sorts of accounts if the issue is causal explanation of particular traits of organisms. They argue for a noncausal approach to teleological explanation, according to which teleological language serves to group together phenomena involving diverse causal mechanisms. According to the Thesis of Multiple Realizability, different microlevel properties can underlie the same functional properties. This means that claims made at the functional level have a higher level of generality than claims that focus on microlevel properties. Teleology, according to Enç and Adams, is concerned with noncausal explanation at a higher level of generality than is provided by the microlevel properties.

Sandra Mitchell, a philosopher as well, also takes up the metalevel question of how accounts of function are to be understood, arguing that before assessing particular accounts of function, it is important to understand the goals of providing an account. Functions, she claims, are not concrete substances like gold, or water, and so it is misleading for Neander and Millikan to use the analysis and definition of substance terms as models for understanding questions about function. On her view, "function" is more like "cause" or "reason"—it is an abstract term that designates an explanatory structure. Instead of asking about the *meaning* of function terms, Mitchell thinks that it is more fruitful to understand the explanatory structure required to make sense of certain functional claims in both biology and cultural anthropology. This structure, Mitchell argues, requires the identification of selection and transmission mechanisms that provide the causal background to explain the presence of traits (including behaviors) in a given population.

In the context of giving this kind of explanation, Mitchell finds difficulties for Bigelow and Pargetter's forward-looking, dispositional account of function. She argues that Batesian mimicry presents a problem for their view because, for example, the coloration pattern of a poisonous butterfly (the Monarch) and its mimic (the Viceroy), have very similar dispositional properties but different biological functions: the function of the Monarch's coloration is to warn predators about poison, whereas the function of the Viceroy's is to mimic the Monarch's. Despite her objections to the view, Mitchell thinks that Bigelow and Pargetter have identified an explanatory concept that is important to biology. Specifically, their account of function corresponds to the explanatory task of saying how a trait contributes to the survival and reproduction of organisms with that trait. In contrast, the etiological account of function corresponds to the task of saying how having the trait has historically contributed to the presence of the trait. Mitchell concludes (p. 411) that "there is not a single, univocal explanatory task for which such language is employed" and that "the philosophical task is to recognize the plurality of explanatory projects, to clarify their relationships, and to explicate their structures." (See also Bekoff and Allen 1995.)

## Synthesis or Pluralism?

Each of the articles in this section attempts to come to terms with the plurality of uses of the term *function* by biological scientists. As an ethologist, Robert Hinde's interest is in behavior. He begins by identifying the functions of behavior as the beneficial consequences to the organism of performing the behavior. He distinguishes between "weak" and "strong" senses of function. Hinde's notion of the weak functional meaning could be construed as an account similar to Cummins'. On Hinde's view: "A weak meaning answers the question 'what is it good for?' … By contrast, 'function' in a strong sense attempts to answer the question 'through what consequences does natural selection act to maintain this character?'" (p. 422). Hinde's strong sense appears to be a version of the etiological account: the maintenance of the trait in the organism(s) is causally explained by reference to natural selection. But in his weak sense of function, what is explained is how a certain trait contributes to some further ability of the organism. Hinde's example is that wings contribute to the capacity for flight. This contribution can be understood independently of knowing how (or even whether) flight contributes to survival and reproductive success, and hence to the presence of the trait. In fact, however, Hinde claims that the weak and strong meanings of function represent the ends of a spectrum, rather than discrete alternatives. Because questions of function are "still too often treated as a matter for speculative asides," Hinde takes up the question of evidence for functional attributions and argues that both observational and experimental approaches are useful, although laboratory conditions tend to support claims about function only in the weak sense.

Philosopher Paul Griffiths seeks to show that the etiologically-defined proper functions of a biological trait can be identified with the functions attributed by a Cummins-style functional analysis of the fitness of the organism's ancestors. A difference for Griffiths between *proper* functions and functions more generally is that the former can be cited to explain the presence of a trait. This is the core of etiological accounts of proper function, yet Griffiths maintains that many of the available etiological theories are flawed. He criticizes Millikan's account for failing to capture the important distinction between a functional trait and a vestige. Neander's view is criticized on the ground that it misrepresents the structure of explanation by natural selection—in particular, Griffiths claims, Neander's account improperly requires an increase in the frequency of genes that code for a trait in order for that trait to have a proper function. Griffiths' own account of proper function invokes the fitness contribution made by a trait's effects that helps to provide a selective explanation for the presence of the trait in the population, and he shows how this idea must be precisely stated to preserve the biologically important distinction between traits with functions and vestigial traits. Because of the explicit role played by the theory of natural selection in his account, Griffiths denies that it is possible to give a perfectly unified account of biological function and artifact function. Nonetheless, a generalization of the notion of selection does, he believes, lead to a "selection-type" theory of artifact function. Ultimately, for Griffiths, it is some form of selection that is responsible for the presence of teleology.

A problem for etiological accounts is the difficulty of saying how far back in history one should go to determine function. That birds' wings are descended from the fins of fish does not show that wings are for swimming. Peter Godfrey-Smith, a philosopher, proposes to solve this problem by stipulating that (p. 453) "Biological functions are dispositions or effects a trait has which explain the recent maintenance of the trait under natural selection." This account is etiological and historical but attempts to draw a line limiting how far back one should go to determine function. Godfrey-Smith also views his project as (p. 454) "conceptual analysis guided more by the demands imposed by the role the concept of function plays in science, the real weight it bears, than by informal intuitions about the term's application." Many ethologists, often citing Tinbergen (1951, 1963), rely on a distinction between evolutionary explanations and functional explanations (see also Brandon, chapter 3). Godfrey-Smith regards this as a potential embarrassment for historical accounts of function. He proposes to remove the embarrassment by granting (as did Millikan 1989) that a certain amount of ahistorical usage of *function* by biologists can be captured by Cummins' account, but that the core etiological sense of function is a type of evolutionary explanation that appeals explicitly to recent propensities that, in the vast majority of cases, should be expected to have continued into the present. In this way, Godfrey-Smith believes he has steered a "principled middle course" between backward-looking and concurrent or forward-looking accounts.

Philosopher Philip Kitcher takes on the multiplicity of theories about function ascriptions, and argues that many of them—including pre-Darwinian conceptions—can be unified through the notion of design according to the schema that "the function of an entity *S* is *what S is designed to do*" (p. 479). According to Kitcher, either natural selection or agent intentions can underlie attributions of function, but the former is more significant for understanding function attributions in biology. He laments, however, that Tinbergen's distinction between "why" questions answered by selection history and "why" questions answered by current function is collapsed by standard etiological analyses of function that appeal to the history of selection as the source of the initial spread of a trait. Kitcher sides with Godfrey-Smith in preferring an analysis of function that looks to recent selection history. Although he regards Cummins-style functional analysis as "too liberal" because any complex system can be subjected to such an analysis, Kitcher, by way of several examples drawn from the biological literature, attempts to show that Cummins-style analysis is an important tool in the attempt to analyze the design of biological systems. Furthermore, because both natural selection and conscious intention can be sources of design, Kitcher believes that he has shown how a single account of function can cover both artifacts and biological entities.

## Design

The notion of design in modern biology has a long history stretching most notably from Hume's (1779) criticisms of all versions—nonbiological as well as biological—of the "argument from design," to Paley's (1802) famous attempt to illustrate that design of any kind implies the existence of a designer, to current biological uses of the concept of natural selection to demonstrate design and function. Evident still in modern biology is the tension between two views: one of design as manifest evidence of the necessity for teleological explanations, the other of design as a result of some process (such as natural selection acting on random variation) that does not require teleology (Dawkins 1987). A pervasive component of many current explanations of biological traits, especially those deemed adaptations, is the notion of design for some function (Rose and Lauder 1996), and biologists seem to have a difficult time escaping the use of teleological language in their descriptions of design. Still, this teleological tension is evident in the papers chosen here by the contrasting views on the nature of design, its origin, and the methods advocated for the analysis of design.

We begin the section on design with a paper by George Lauder, who tackles what he calls "the problem of biological design"—the twin problems of explaining why relatively few of the theoretically possible phenotypes have actually evolved and of formulating testable explanations for why some morphological forms have not evolved. Design and (implicitly) function are distinguished from adaptation by the involvement of natural selection in defining *adaptation*: Lauder defines design (p. 508) as "the organization of biological structure in relation to function" whereas adaptation "is restricted to features that have arisen by means of natural selection." According to Lauder, the most common approach to the problem of design is to take a mechanical or biochemical approach to the relationship between form and function that sees organisms as in equilibrium with environmental forces. An alternative approach analyzes biological structures historically in an attempt to discover the intrinsic determinants of evolutionary change, that is, those features of organisms that facilitate morphological change in certain directions but inhibit changes in other directions. (For example, one might try to explain why it is that, despite independent origins, the wings of bats and the wings of birds both evolved from forelimbs rather than hindlimbs: is there something intrinsic to the vertebrate body plan that favors the evolution of forelimbs into wings and blocks the evolution of wings from hindlimbs?) Lauder claims that the problem of biological design is fundamentally historical. Although the historical approach is more difficult because it is harder to test, Lauder argues that the goals of historical morphology can be effectively carried out by selecting general (not unique) features for explanation, explicitly formulating hypotheses about the phylogenetic sequence of feature acquisition, and examining related monophyletic lineages (lineages containing all the descendants of a given ancestor).

Biologists Stephen Jay Gould and Elisabeth Vrba also have the needs of morphologists in mind as they set out to clarify the term *adaptation* and to argue that evolutionary morphologists need new labels for related concepts. They distinguish adaptation in the sense of "the historical processes of change or creation for definite functions" (p. 520) from adaptation in the sense of the utility of a trait for an organism in its current environment, for which they prefer to use the term *aptation*. Gould and Vrba describe traits of organisms which were originally adapted for some function (e.g., feathers for insulation) but then coopted for other effects (e.g., for insect catching) in the course of evolution "that sets the basis for a subsequent adaptation" (e.g., for flight). At certain intermediate stages, although the later adaptive changes have not yet occurred, the basis for these changes is present, and here Gould and Vrba suggest using term *exaptation*. Thus, feathers were initially adapted for flight and exapted for insect-catching; changes due to selection led to adaptation for insect-catching and exaptation for flight; further changes result in adaptation for flight. Exaptation may also appropriately describe nonadaptive traits (or *nonaptations*) that are coopted for a particular effect when the opportunity arises—the opportunistic nature of this process eliminates any suggestion of teleological directedness. Gould and Vrba argue that, in contrast, the commonly used *preadaptation* has awkward connotations about preordination of future adaptations, and they suggest that the term *preaptation* more accurately captures the idea that a trait may be the substrate for future adaptive development. Gould and Vrba suspect that evolutionists have not formally recognized the concept of exaptation because they have overplayed the claim that adaptation is the primary driving force in evolution, and have fallaciously drawn inferences about historical genesis from observations of current utility. In their view, exaptations that begin as nonaptations may be of far greater importance for understanding evolution.

In the next chapter, morphologist Carl Gans defends the view that adaptation is the primary basis for understanding "the match of form and function" which is advantageous to organisms, an idea that Gans traces to pre-Darwinian times. Gans nods toward Bock and von Wahlert's separation of function and biological role, but proceeds to use *function* to mean what they meant by *biological role*. He then notes the ambiguity in the term *adaptation* (also noted by Gould and Vrba, chapter 20) between, on the one hand, the present state of an organism being more or less well equipped to survive in its current environment and, on the other hand, the historical process of becoming adapted in the first sense. Gans contends that many of the worries about adaptationism—a thesis about the capacity of natural selection to account for the phenotypic properties of organisms—are derived from an inadequate appreciation of the distinction between the two senses of adaptation. Gans wisely rejects any identification of adaptation with perfection and tackles the question of how hypotheses about adaptation can be tested.

Although many authors who accept an etiological account of function treat the notions of function and design inseparably, philosopher Colin

Allen and ethologist Marc Bekoff argue that not only can these notions be separated, they should be, as their separation helps articulate important issues in the evolution of morphological and behavioral traits. The definition they offer is based on an etiological account of function, although they acknowledge that other conceptions of function have roles to play in biology. Allen and Bekoff adopt an etiological conception of function which they claim does not require any special adaptation of the trait for its function. If, for example, eagles use their wings to shade nestlings, this could be considered a function for which the wings have not been specifically designed. In contrast, when adaptive change has occurred in the trait through natural selection, making the trait more optimal or better adapted for the performance of the function, then it becomes appropriate to say that the trait is designed for a function. Thus, the glide ratio of eagle wings can be compared to the glide ratio of the wings of eagle ancestors. If an eagle's wings result in a higher glide ratio than its ancestor's wings and having a higher glide ratio provides a comparative fitness advantage, then it can be said that the eagle's wings are designed for soaring. Allen and Bekoff motivate many of their claims about design by means of direct comparison to psychological cases of design, but they insist that biological design should be analyzed separately from psychological design. They end their paper by considering the role of comparative studies in assessing claims about design, and the particular difficulties in the area of animal behavior due to the lack of fossilized information about behavior.

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