PREFACE

When the present book project was reviewed, some reviewers suggested the best thing would be for me to write a book on the character concept on my own. I did not follow this advice, and the contributions collected in this volume show I made the right decision. The problems associated with the biological character problem are so complex and multifaceted and this issue is so conceptually immature that any single author's account is doomed to be too narrow and lopsided to be of much use. I am convinced that only the interaction between the results from many model systems and techniques, the ideas of many people, and the productive criticism among colleagues will yield progress in this difficult conceptual territory.

The collection of papers united in this volume is intended to do exactly this, namely, bring together results and ideas from philosophy of science, evolutionary theory, systematics, genetics, functional morphology, and developmental biology which have implications on the way we conceptually construct and identify characters in biology. Not all authors agree on their perspective on the character concept. This is expected and good. I hope that this juxtaposition of ideas will stimulate further discussion of their merit, and ultimately stimulate the creative replacement of these ideas with better ones. If this ever happens, the present volume will have served its purpose.

I want to take this opportunity to thank all the authors, who have contributed excellent papers to this book. Their creativity makes reading the book such an

intellectually rich experience. I also want to thank Richard Lewontin, who was kind enough to write a foreword in which he put our project into the proper intellectual context. My thanks also go to Chuck Crumly, who has shepherded this project through its various ontogenetic stages, and especially to Paulette Sauska, who did the most exhaustive and exhausting task of editing and formatting the manuscripts for print. Without her skill and dedication, the project would have died an agonizing death long ago.

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GPW
July 2000
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FOREWORD

"Like following life through creatures you dissect, you lose it in the moment you detect." Already in the 18th century, Alexander Pope had expressed the fundamental problem in the study of living beings, a problem that continues to plague us. How are we to apply an analytic method to living objects in such a way that the phenomenon we wish to understand is not destroyed in the very process of analysis? What are the "natural" suture lines along which we can dissect the organism to understand properly its history and function? For Pope to dissect a creature meant only to cut it up with a knife, but for the modern biologist, and especially the evolutionist, the problem is conceptual. It seems that we cannot carry on our business without using characters, yet there is nothing more dangerous to the proper understanding of biological processes than that first act of characterization. How are we to recognize the "true" characters of organisms rather than imposing upon them arbitrary divisions that obscure the very processes that we seek to understand? That is the question of this book. No issue is of greater importance in the study of biology.

Modern biology is a battleground between two extreme ontological and epistemological claims about living creatures, claims that reflect the history of biological study. One takes as its model the physical sciences and their immense success in manipulating and predicting the behavior of much of the inanimate world. In

that domain there are a few basic laws governing all phenomena, the laws of Newton and Einstein, of thermodynamics, of electromagnetic theory, and of nuclear forces. The objects of study either are universal elementary bits and pieces, particles, atoms, and molecules or are composed of those bits and pieces in an unproblematical way. They are Cartesian machines, clocks that can be understood by looking at the articulation of the gears and levers that are clearly recognizable as their parts. It is the extreme reductionist model that validates the various genome-sequencing projects. When we possess the complete description of the DNA sequence of an organism, we have all the information we need to understand the organism. This extreme molecular reductionism is the outgrowth of the 19th-century program to mechanize biology, to expunge the vestiges of mysticism from the study of life, and to bring that study within the domain of universal physical law. Darwinism, Mendelism, biochemistry and biochemical physiology, and Entwicklungsmechanik were its intellectual precursors.

At the other extreme is a radical holism that denies the possibility of learning the truth through analysis. The living world is a seamless whole and any perturbation of one bit of the living world may be propagated in unpredictable ways throughout the biosphere and certainly throughout the entire physiology of any individual organism. It is the whole as whole that must be studied. The belief in this holism has been greatly fortified by the discovery of chaotic regimes in fairly simple dynamical processes, showing that even minor perturbations may give rise to apparently unpredictable dynamical histories. In an attempt to make holism a science there is a movement to develop a mathematical theory of "complex" systems in the hope that complexity will have its own, irreducible laws. Modern "scientific" holism is a return to the obscurantist holism that informed biology before the middle of the mid-19th century and the romantic organicism and naturalism that opposed the development of mechanistic biology, tainted by the stench of the "dark Satanic mills."

Both extreme reductionism and holism escape the character problem. For the reductionist the characters are obvious and unproblematical. They are molecules and distinct sequences of molecular interactions. There is a signaling pathway, composed of controlling regions of DNA in certain genes and proteins coded by other genes, that determines the differentiation of a particular part of an embryo. The part is unproblematical because it is the outcome of the operation of a distinct and well-defined autonomous collection of genetic elements. If genes determine organisms, then parts of organisms are defined by the autonomous assemblages of genes that cause them. One of the ironies of the perverse history of scientific language is that, in its original sense, this reductionism is a truly organic view. The use of the word "organism" for a living being and the "organic" view of life were originally metaphors likening the body to the musical organ, a system of well-defined articulated parts that contribute to the operation of a whole. Nothing is more transparently clock-like and easy to break down into separate functional parts than a musical organ. The keyboard, the foot pedals, the bellows, each set of pipes are all clearly separate organs (in the biological sense) with easily defined

relations among them. Indeed, except for the source of air all the parts can be individually disabled without interfering with the operation of others. If the vox humana stop is inoperative, nothing prevents the organist from playng the entire program with the flauto, and if the keyboard is not working, the foot pedals will still serve to play the tune. If bodies were really organic, the problem of characters would not exist and biology would be a simple science. Radical holism, on the other hand, finesses the problem of characters by denying their real causal existence, making of them merely mental constructs. Their text is Wordsworth:

> Our meddling intellect
> Mis-shapes the beauteous forms of things:—
> We murder to dissect.

Because everything is connected to everything else, the delineation of characters is necessarily arbitrary and ultimately destructive of the truth. Moreover, it leads us to a dangerous hubris about how we safely intervene in the world.

The problem for biology is that neither a radical holism nor an organic reductionism captures the actual structure of causation in the living world. It is clearly not the case that everything is connected effectively to everything, even in the relatively simple world of physical objects. Gravitational forces are everywhere, but because gravitational force is weak and falls off with the square of distance, the entire universe of objects is not locked up in an effective gravitational whole. I can feel quite confident that the motion of my body exerts no effective gravitational pull on the person who passes me in the street. It cannot be that the alteration of every part of the body of an organism has a palpable functional or developmental effect on every other part or else evolution could never have occurred. Selection on every bit of the organism would result in simultaneous pressure on every other bit, requiring the organism to be totally rebuilt in response to every selective change. Nor can every species community be totally overturned if one or another species drops out of the mix, although large perturbations may sometimes happen. Despite the popular wisdom, the death of a single butterfly in Madagascar will not have effects propagated throughout the living world or else the temporal instability of the biosphere would have long since resulted in the extinction of all life.

It is necessarily the case that the material world is subdivided into relatively small sets of objects and forces within which there are effective interactions and between which there is operational independence, what has come to be called "quasi-independence." This fact immediately predisposes us to both a conceptual and a methodological reductionism. Let us break down organisms into the smallest pieces we can and then slowly put them back together again, a bit at a time, to see which parts are, in fact, in effective interaction with each other. We can then map out the quasi-independent subsets, the natural characters that constitute living systems. No one can deny that this methodological reductionism has had great success. Everything we know about biochemistry and physiology, about basic cellular mechanisms of replication, about development, has been learned by taking

things into pieces and putting them back together again. That is how we know that the differentiation of digits from a limb bud is independent of the differentiation of the external pinna of the ear or that the metabolism of alcohol as affected by the enzyme coded by the alcohol dehydrogenase gene is physiologically separable from the formation of eye pigment in *Drosophila*. That digits and ear pinna or alcohol and eye pigment biochemistry are different characters in the developmental or physiological sense need not have been the case. It simply turned out that way and we would not have been forced to reorganize our understanding of biology had things turned out differently. Methodogical reductionism seems to work, so why not pursue it as a program and let nature speak to us, delineating characters for us bit by bit? We do not do this because it is the failures of a method, not its successes, that are its test.

Organisms occupy a special part of the property space of physical objects. First, they are intermediate in size between plants and particles. Second, they are internally functionally heterogeneous, being composed of many subsystems at many levels. There are different species of molecules in the cell, spatially localized in organelles and cellular regions, and, in multicellular organisms, different cells in each organ and different organs with different functions. Third, many of the molecules and organelles in cells are present in extremely low numbers and so their reactions are not described statistically by the laws of mass action. The consequence of these properties is that organisms are the nexus of a very large number of individually weakly determining causal forms and are subject to stochastic uncertainty. What is true for one organism at one time may not be true for others at other times and in other circumstances. The obvious successes of the reductionist program are precisely in those cases where little or no difference can be seen between different organisms, like the discovery that genes homologous to the *Hox* genes of *Drosophila* are involved in anterior–posterior differentiation in an extraordinary diversity of organisms. But along the way molecular reductionism has also found an undoubted heterogeneity of causal relations from organism to organism and from circumstance to circumstance.

We might, for example, ask what the relationship is between the amino acid sequence of a protein and a functional property that would be regarded as an evolutionary character. No demonstration of the operation of natural selection is more compelling and unambiguous than the discovery by Kreitman (1983), nearly 20 years ago, that the amino acid sequence of the alcohol dehydrogenase gene in *Drosophila* was totally constrained, except at a single amino acid position, while the silent sites in the codons of the gene were 7% polymorphic. We require no assumptions about natural history or physiology to conclude that natural selection is weeding out essentially every amino acid substitution, even such a priori functionally equivalent substitutions as leucines, isoleucines, and valines. Yet this strong molecular demonstration of highly discriminating natural selection in one case turns out not to be general. Many similar studies on other genes in *Drosophila* have since shown a great diversity in the discriminatory power of natural selection on amino acid sequences.

Nor is there any clear relation between the qualitative properties of a protein and its amino acid sequence. At one extreme almost the entire amino acid sequence of a protein can be replaced while maintaining the original function. Eukaryotes, from yeast to humans, produce an enzyme, lysozyme, that breaks down bacterial cell walls. In the evolutionary divergence that has occurred in the yeast and vertebrate lines since their ancient common ancestor, virtually every amino acid in this protein has been replaced, so an alignment of their two protein or DNA sequences would not reveal any similarity. The evidence that they are descended from an original common ancestral gene comes from comparisons of evolutionarily intermediate forms which show more and more divergence of sequence in species that are more divergent. The maintenance of the function despite the replacement of the amino acids has been the result of the maintenance of the three-dimensional structure of the enzyme by the selective substitutions of just the right amino acids.

In contrast, it is possible to change the function of an enzyme by a single amino acid substitution. The sheep blow-fly, *Lucilia cuprina,* has developed resistance to organophosphate insecticides used widely to control it. R. Newcombe, P. Campbell, and their colleagues (Newcomb *et al.,* 1997) have shown that this resistance is the consequence of a single substitution of an aspartic acid for a glycine in the active site of an enzyme that ordinarily is a carboxylesterase. The mutation causes complete loss of the carboxylesterase activity and its replacement by esterase specificity. A three-dimensional modeling of the molecule indicates that the change is the result of the ability of the substituted protein to bind a water molecule close to the site of attachment of the organophosphate, which is then hydrolyzed by the water.

These examples show both the power and the weakness of methodological reductionism for the problem of characters. The method is immensely powerful in reconstructing individual stories but the very diversity that it reveals deprives us of any hope of generalization at this level. Every case will be different. As lawyers say in answer to almost any question posed in a general context, it depends on the jurisdiction.

The alternative strategy is to search for patterns in the manifest properties of a great diversity of organisms of known or inferred relationship. Of course, there is always the danger of circularity, since characters are used to infer relationship, but this tautology can be broken by using a completely different set of properties to establish the phylogeny, say molecular data, and then searching for patterns in morphology or complex behavior. Characters can then be delineated by the properties that show strong correlations or conservations across organisms. Many of the essays in this book deal with this approach to understanding evolutionary characters.

Characters defined (or detected) by the observation of correlations are thought to be given coherence by two possible constraining forces. First, there are developmental constraints. Somehow in the developmental process an increase in one dimension or property is necessarily accompanied by an increase or decrease

in another. General changes in size are often invoked (bigger deer have bigger antlers) but biochemical relations may also be constraining. Despite great efforts on the part of plant breeders no one has ever succeeded in breaking the positive correlation between tar and nicotine content in tobacco or the negative relation between protein content and yield in soybeans. Second, there are functional relations. Natural selection builds characters. If the shape and size of the mammalian ear ossicles did not evolve as a unit, each fitted to the other, aural acuity would be compromised, with, presumably, some loss of fitness. As an extreme of the natural selective explanation, there may be an absolute dependence on a fit between two structures for any development at all to occur. Thus, we expect coevolution of DNA binding proteins and their binding sites in signal transduction pathways of early development. Binding protein and binding site are a single evolutionary character.

The problem with this dichotomization is that it is insufficiently evolutionary and insufficiently contingent. In the first place, developmental constraints between parts are not generally global but local in the space of genotypes. Even when a correlation appears to be as simple as one arising from total size variation, there may have been natural selective forces responsible for building it and there may even remain within species sufficient genetic variation to reverse it. An example is the length of various stiffening veins in the wings of *Drosophila*. The lengths of these veins are positively correlated within and between species and remain correlated if the flies are raised at different experimental temperatures, so shape remains constant as size varies environmentally and phylogenetically. Nevertheless, Haynes (1988) succeeded in reducing and even reversing these correlations by artificial selection in *Drosophila melanogaster,* showing that in a region of genotypic space accessible to the genus there was the possibility of a change in shape. Moreover, the unit of selectable morphology in these wings is extremely small. Weber (1992) was able to change the angle and lengths of veins in a region of only about 30 cells by selection, while leaving the rest of the wing unchanged.

Second, functional units are created by the life activities of the organism and vary from circumstance to circumstance. The loss of the last joint of my left little finger would be totally inconsequential for any function that I perform and would surely go unrecognized by natural selection, but it would be of considerable consequence indeed if any livelihood depended on playing the violin. At one moment the entire hand is a character, at another each finger is a character, and at another the hand and arm form a single functional unit. Whether particular agglomerations of bits and pieces of the organism are characters in evolution is not determined by some autonomous external prior circumstance, but by the mode of life constructed by the organism out of the available bits. The green turtle, *Chelonia mydas,* uses its hind flippers to dig a hole in the sand in which to lay its eggs, but no one who has observed that laborious and clumsy process can imagine that natural selection produced those hind appendages as an adaptation for digging. Nevertheless, it is reasonable that some alteration in those organs, chiefly used for swimming, has occurred as a compromise with their use on land. There is a constant evolutionary

feedback between the characters that organisms use to make a living and their mode of employment. The environment of an organism comes into existence and changes simultaneously with changes in morphology, physiology, and behavior of organisms. Any concept of evolution that does not take the properties of the organism as both the cause and the effect of natural selection will fail to solve the problem of the character in evolution.

R. C. Lewontin

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CHARACTERS, UNITS AND NATURAL KINDS: AN INTRODUCTION

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INTRODUCTION

Organisms owe their special status as living beings to their material organization. There is no special force or substance that distinguishes organisms from inanimate matter; only everyday physics and chemistry prevail in the details of an organism's life. The difference between inanimate matter and organisms thus lies in the spatial and temporal organization of ordinary physical and chemical processes. The contents of the cell need to be separated from the environment, and inside higher cells compartments need to be neatly separated and the exchange of molecules among them tightly regulated to ensure the continuation of life. This implies that spatial and temporal heterogeneity is fundamentally linked to the existence of life as a material process. This intrinsic need for heterogeneity and the tendency of organisms to increase the heterogeneity of their material organization during ontogeny and phylogeny has been recognized by humans ever since our ancestors started to give names to

things in their environment. I guess that the recognizable parts of humans, animals, and plants must have been among the first things that received names, such as hand, head, and eye, because they are of fundamental importance to the life of all peoples. This is also the origin of the character concept, i.e., the idea that organisms consist of natural units, which, in some cases, can even be identified in organisms of different species. Once this step was taken, namely to recognize that essentially the same parts can be found in different species, the idea of homology had been born. Characters are thus among the most fundamental units we use to systematize the things in our world, together with ideas about species, and different forms of matter such as air, water, and stone. Surprising then is the relative lack of attention the character concept has received (but see Gould and Lewontin, 1978; Lewontin, 1978; Ghiselin, 1984; Colless, 1985; Rosenberg, 1985; Rodrigues, 1986; Inglis, 1991; Stearns, 1992; Wagner, 1995) compared to the species concept or the concepts that form the core of the inorganic sciences. The purpose of this collection of essays is to put the character problem into the context of mechanistic biology in order to aid the development of a scientific character concept.

Only in one incarnation did the character concept receive extensive attention, namely in the context of the homology problem. The homology concept has a long but frustrating history. Only a temporary ceasefire has been reached with the introduction of cladistic methods in systematics. Cladistics gave some operational meaning to the notion of homology (Patterson, 1982). The breathtaking progress of developmental genetics, however, reignited the debate over issues that could largely be ignored in a cladistic context. For instance, what is a homologue and what accounts for its identity? The progress in developmental genetics only magnifies the problems that had already been seen by perceptive thinkers such as Spemann (1915), deBeer (1971), Riedl (1978), VanValen (1982), and others. The unsatisfactory status of the homology debate, I think, is a consequence of the fact that the debate about homology happens in a much too narrow context. The question usually asked is "How do I recognize the character in species B that corresponds to the one I know from species A?" This is an important problem for many areas of biological research, but is much too narrow compared to the scope of the problem: what are the natural unit organisms composed of? How do we recognize these units? How do we justify our choices? What is the theoretical context in which we can make these choices? Why do they exist? How did they come into existence?

In this introductory chapter I want to outline some of the theoretical background for the essays collected in this book. Why does biology need a character concept? What is the conceptual framework for addressing the character problem? What are the research problems that need to be attacked? The answers to these questions will also explain the motivation behind the present book project. I expect that a close reading of and reflection on the chapters in this book will lead to a fundamental revision of the views that I

express in these pages, which is exactly the purpose of theories: inducing research that makes them obsolete.

WHY DOES BIOLOGY NEED A CHARACTER CONCEPT?

Despite the widely acknowledged functional and organizational wholeness of organisms, biology concerns itself largely with the study of often minute parts of organisms. Even so-called organismal biology mostly deals with either physical or functional parts or with abstractions of organisms such as life histories, populations, or behavioral patterns. The success of a research program depends to a large degree on the right choice of the parts or abstractions to be studied. The cell, for instance, is an example of a subsystem of higher organisms, which has all the hallmarks of a natural unit. It has a high degree of internal coherence and exhibits emergent properties that play a prominent role in the explanation of biological phenomena. On the other hand some of the intensively studied quantitative abstractions of classical physiology did not lead to generalizations because the fundamental units are often molecular or cellular rather than systemic. Hence, the identification of natural (sub)systems of organisms stands at the beginning of every research program in biology and influences its success.

The few examples of characters mentioned earlier suggest a preliminary definition of a character that could temporarily serve as a guide through the jungle of ideas and observations around the character concept:

A biological character can be thought of as a part of an organism that exhibits causal coherence to have a well-defined identity and that plays a (causal) role in some biological processes.

This (pseudo) definition is radically more ambitious than the narrow definition of a character in systematics. In systematics, characters are conceptualized as any observable difference between two groups of organisms, which can be used to "characterize" (distinguish) these groups. Our definition aims at the question why it is at all possible to individuate meaningful characters within the context of the functional integrity of the organism. What are the mechanistic conditions that make the idea of characters meaningful? A very general reason has been given in the first paragraph of this chapter, namely the need for organisms to spatially separate various processes. However, this is of course by far not sufficient because it does not provide us with an idea of how to find and individuate these characters and to formulate a research program into the nature and evolution of these units.

Of course there are parts of organisms which clearly fulfill the criteria of this definition, namely molecules and cells, and they are the subject of well-established scientific disciplines: biochemistry and cell biology. Is anything else

needed? I think there is one main reason that indeed more is needed: organisms exhibit multiple levels of integration. Potentially at each level of integration units can exist that exhibit sufficient coherence and play a causal role in a process to warrant their recognition as a character. As pointed out by Robert Brandon, mechanisms can arise at any level of integration, and the assumption that mechanistic explanations can only come from smaller (molecular) units or higher units is a metaphysical commitment that has no place in science (Brandon, 1996). I suspect that the things that we call characters, defined at a certain level of integration, are the players in emergent mechanisms that occur at the respective level of integration. The existence of emergent levels of complexity with their level-specific causality seems to be generic property of complex systems (Bar-Yam, 1997).

To illustrate this point I want to recount Philip Kitchers metaphor of the reductionist madman. Kitcher uses the phenomenon of the 1:1 sex ratio in human populations to point out that the most informative explanation is the one originally given by R. A. Fisher, namely that there is frequency dependent selection for equal proportions of male and female offspring (Fisher, 1930). Only a madman (or madwoman) would in all seriousness consider a fully molecular account of this phenomenon. Such an account would need to explain how it comes that about the same number of Y chromosome and X chromosome bearing sperm are successful in fertilizing an egg and that during development the right proportion of fetus die such that in the end we have a sex ratio close to 1:1. Clearly, population genetics provides a mechanistically much more meaningful explanation than a molecular account. I take this example as an illustration for the existence of causally relevant mechanisms at higher levels of organization.

If causally relevant mechanisms exist at higher levels of organization, then it becomes interesting to ask what are the units that play a causal role in these mechanisms. I guess that most of the units that strike us as sufficiently distinct and coherent parts (i.e., characters) are those units. Otherwise it is hard to understand why these units exist at all (Wagner, 1995).

A well-developed character concept could thus help us eliminate metaphysical commitments, such as the idea that mechanistic explanations can only derive from the molecular level of description. There are of course mechanisms at the molecular level which are of fundamental importance to all aspects of life; this is not the issue. The issue is whether these molecular mechanisms are the only ones that matter in biology. This is not a metaphysical question but an empirical one.

Before I consider how other sciences define their fundamental units and what biology may learn from it, I want to discuss two biological problem areas that could benefit from a better understanding of the character problem. One is the genetic explanation of morphological variation and the other is the empirical meaning of mathematical models in biology. The problem of a genetic explanation of morphological differences between species is nicely illustrated by

the debate surrounding the discovery of homologous genes involved in the development of very different light sensory organs (eyes) (Bolker and Raff, 1996; Müller and Wagner, 1996; Abouheif, 1997). Halder and collaborators (1995) have shown that the gene *Pax-6* is sufficient to initiate the development of compound eyes in the ectoderm of *Drosophila melanogaster*. What is remarkable though is the discovery that a homologous gene exists in mammals that is also necessary for the development of the "camera" eye typical of vertebrates. The eyes of mammals and flies, however, taken as anatomical characters, are certainly not homologous. Their structure is too different and mammals and flies too distantly related that either was derived from the other. Most likely both are derived from a common ancestral structure, which was neither a compound eye nor a camera eye, but maybe only a light-sensitive epithelium. The ancestral role of *Pax-6* homologues then most likely was to initiate the development of the light-sensitive epithelium, which is the phylogenetic precursor of both the camera and the compound eye. In derived species the ancestral structure became transformed into what is now either a compound or a camera eye, neither of which is the same as the ancestral structure. The role of *Pax-6* in derived species then is to determine the eyefield, i.e., the ontological precursor of complex, derived eyes. As Riedl has said so perceptively: the phylogenetic precursor of a derived character corresponds to the ontogenetic precursor of the same character in derived species (Riedl, 1978). To solve the riddle of homologous genes causing the development of nonhomologous characters requires a careful distinction between the levels of organization and the kinds of characters involved. An eye is not necessarily an eye. A clearer understanding of the biological meaning of character identity would be useful to sort out problems like these.

Another example of how a character concept might be useful in biological research is the interpretation and the empirical testing of mathematical models. The ambivalent opinion of most biologists toward mathematical models is in part caused by a structural weakness of these models (the other part is the complete lack of mathematical training). Mathematical models are an absolute necessity in many parts of biology, in particular in organismal biology, where the processes investigated are often quantitative and hard to put into a lab setting (just like in cosmology). The best examples are population biology and ecology. In Laubicher and Wagner (2000) we have argued that the models in these areas have a structural weakness because they lack a clearly defined theory of what their intended range of application is. Under exactly what conditions can we apply a life history model? What exactly are the life history characters, and how can we test whether a particular system is a legitimate instance of the model? All these questions derive from a lack of understanding of what units play a mechanistic role in a certain process. In other words, all these questions ask about what the relevant characters are for the focal mechanism.

NATURAL KINDS AND BIOLOGICAL MECHANISMS

As argued earlier, the character problem can be seen as a special case of a problem that occurs in many (all?) sciences, not only in biology, namely the question of what fundamental units play a causal role in a process. The most general form of this problem is the so-called natural kinds problem (Putnam, 1981; Keil, 1989; Boyd, 1991; Hacking, 1991; Wagner, 1996; Griffiths, 1997). In this section I want to discuss how the notion of natural kinds, as developed in other sciences, can help in guiding our thinking about the character concept.

In a seminal essay, Quine (1969) has reflected on the conceptual nature of those units which play a fundamental role in the theoretical core of a science, such as atoms and molecules. Most of the essay is dedicated to the discussion of various proposals to define natural kinds, such as similarity or statistical considerations, and he rejects all of them. Toward the end of the essay, however, and almost in passing, Quine makes a startling suggestion. He simply suggests that natural kinds are things that play a role in a law of nature. No other definition would work. In other words, natural kinds are defined by their function in interacting with other such kinds, not by their intrinsic characteristics alone. One has to appreciate that Quine's argument was formulated in the linguistic tradition of the philosophy of science and contains concepts that seem problematic from our point of view, in particular the notion of a "law of nature." I think it is fair to translate Quine's formulation into a more realistic interpretation: a natural kind is a unit that plays a mechanistic role in a process. Nothing essential has been lost in this reformulation.

A major challenge to the natural kinds concept came from Putnam (1981), who pointed out that there is no finite list of attributes that allows us to define a natural kind. His favorite example is the chemical element *Au*, gold. For instance gold could be defined among other attributes by its color. The color, however, is not a constant attribute, since evaporated gold has no color and pulverized metallic gold is black. I think a solution to this problem suggests itself from considering how chemists in fact identify and thereby operationally define chemical elements and substances. Textbooks of chemistry tell us that gold is defined as a chemical element of atom number 79. This in itself is not very useful since it only replaces one abstraction by another. What we need to find out is what gives these abstract concepts their empirical meaning. Looking back on my training as a chemical engineer I suggest that any expert does in fact identify a chemical substance or a chemical element by checking a list of attributes, apparently contra Putnam. The reason why the chemist is nevertheless not falling into the trap Putnam has pointed out is that the chemical attributes that matter in the identification of chemical elements are dispositional properties. That means that they are not just observable properties, but

properties that are expected to be observed if the object is put in a particular situation. For instance, in modern chemistry a lot of chemical identification is done by spectroscopic methods. If I heat a substance containing sodium, *Na*, I expect that it will emit light with a 589-nm wavelength. The same is true of the classical chemical methods, which also test dispositional properties, such as solubility in water and acids or melting point of crystals and reactions with other chemicals. The whole system of chemical elements was erected by defining lists of dispositional properties, each of which stood for and operationally defined a chemical element. The identification of a chemical element with an atomic model was a much later achievement. What this latter conceptual step did was to summarize the lists of dispositional properties in a mechanistic model, i.e., the atomic model.

If we step back and ask what the structural features of this example are, one can recognize three distinct steps in the conceptualization of a natural kind.

1. At the beginning stands, in accordance with Quine, the choice of a class of processes, in the case of chemistry the transformation of matter at moderate temperature levels. (Now we know that chemistry describes transformations of matter at a temperature range in which atoms are stable.)

2. The next step is the identification of stable sets of dispositional properties. The existence of these stable sets is then taken to suggest that there are discrete units that exhibit these properties. These units are hypothesized to be the units participating in the focal processes. Of course the dispositional properties used to define these units are ones that have relevance in the focal class of processes. In chemistry these are mostly reactivities (i.e., if you combine A and B you get C and D). At this stage the natural kind concept is operationally defined but still lacks a mechanistic explanation. Note that the latter is not necessary for the scientific validity of these concepts.

3. The last step is the formulation of a model which explains why the sets of dispositional properties that define natural kinds are stable. In chemistry this is the atomic model, which in fact does explain large chunks of empirical knowledge.

Note that there is not just one natural kinds concept but at least two historical stages: the operational definition and the theoretical model. I think this distinction between two stages of a natural kinds concept may be useful in thinking about biological characters and perhaps even other biological concepts.

Applying these ideas to the biological character problem has a number of implications. The first and perhaps most important is that any attempt to define a character has to start with defining the reference process in which this character is supposed to act as a unit. In many of the traditional uses of the character concept the implicitly assumed reference process is evolutionary change by

natural selection, but this is not universally so, and many conflicts between different character definitions seem to come from a lack of agreement what the implicitly assumed reference process is (Fristrup, this volume). Examples are the process of inheritance, where Mendel discovered that genes are the units of transmission in sexually reproducing organisms. Note that in accordance with our scheme described previously that the classical definition of a gene was based on operational criteria based on crossing experiments. Only later did a model of how molecular structures can account for the Mendelian rules lead to a more mechanistic gene concept. In physiology and functional morphology the reference processes are physiological processes (see contributions by Wainwright and by Schwenk in this volume).

The second implication of the analysis of the natural kinds concept is that the defining properties of characters should be dispositional properties that are relevant to the reference process. In the case of genes this property is the segregation behavior in various crosses. In behavioral biology and physiology the relevant property can be that a sequence of actions can be triggered by a limited set of stimuli, for instance.

The third implication is that the set of dispositional properties has to be based on a causally homeostatic mechanism (Boyd, 1989; Keil, 1989; Boyd, 1991; Griffiths, 1997). In other words, the mechanisms which explain the dispositional properties have to be itself invariant in the reference process. For instance, the structure of an atom (i.e., its nucleus) does not change in chemical transformations, which only affect the structure of the electron shell. A gene is not changed by recombination and a cell keeps its integrity in (most) developmental processes.

The latter point is an important liberalization to the classical notion of natural kinds which was and is often expressed in fairly absolute terms (see chapter 7 in Griffith, 1997, for a discussion). Natural kinds are expected to have a certain degree of stability (causal homeostasis), but the stability is only relative to the interactions in the reference processes. Atoms are invariant during chemical transformations, but not in radiochemical reactions and at very high temperatures. Genes are invariant with respect to genetic transmission but not with respect to mutation. This is important, as biological characters can be quite conservative, as comparative anatomy is showing, but the conservation is of course not absolute, otherwise innovation and body plan evolution would not be possible. Hence characters are less stable than many atoms (but on what common scale?), but the difference is gradual rather than absolute.

If we try to rethink the character problem along those lines it becomes clear that this approach provides a lot of conceptual freedom to explore various options.

FROM CONCEPT TO RESEARCH PROGRAM

A character concept will only be integrated into the body of scientific thinking if and only if it somehow aids the acquisition of further scientific knowledge. A character concept that only satisfies the aesthetic predilections of theorists is ultimately doomed, regardless of how true or elegant it may be. Hence a character concept in itself cannot be the subject of a viable research program if it does not serve a wider purpose. Based on the discussion in the last section, it is clear that any character concept will be contingent on the process in which the characters are expected to play a role. This is true for all areas of biology, as hinted to earlier, but this book focuses on the character concept in evolutionary biology and thus to characters as defined relative to the process of evolution. Hence the character concept aimed at here is supposed to aid research in evolutionary biology and its associated areas such as systematics and other branches of comparative biology. It is a great advantage for the development of the evolutionary character concept that we already have a fairly sophisticated understanding of the elementary mechanisms of evolution. Any character concept thus has to fit into the existing theoretical framework of evolutionary biology, which strongly limits the range of viable candidates. A concept will have to reflect the fact that spontaneous generation of variation and sorting of variants by population dynamic processes are the elementary mechanisms of evolution. With this guideline in mind, a character concept will have to define research programs to answer at least the following three questions:

1. What is the explanatory role of characters in evolutionary theory? I will not seriously attempt to answer this question here, but only want to point to a few directions in which answers may be found. Picking up on Lewontin's idea of characters as quasi-indepent units of evolution (Lewontin, 1978), it may turn out that characters, properly defined and delineated, are the real subject of adaptation. They are the units that interact, within the context of the organism, with the environment and "answers" to adaptive challenges. In turn, if characters are units of evolutionary change, they may be seen as providing each other with the context in which they adapt to the environment. Interactions among characters in the adaptive process would thus be an important part of the explanation of adaptive evolution. Characters with their stable properties are thus the players that form the frame and the context of the adaptive dynamics. As a consequence, the acquisition of certain characters may have long-lasting effects on the diversification of a clade, which is the intuition behind the (controversial) idea of key innovations (see Galis, this volume).

2. What are the mechanisms underlying the causal homeostasis of characters? Assuming that indeed characters play an explanatory role in evolutionary processes, one has to assume that the relevant properties of characters are stable in these processes. Otherwise it would not be guaranteed that a reference to

different instances of a character means the same thing. This in turn raises the question of what mechanisms cause the conservation of these properties. Mutation is random, in first approximation, and selection is opportunistic and variable. Why then would any aspect of the organism be more stable than any other? The answer to this question may lead to a mechanistic understanding of character identity (homology).

3. How do characters come into existence during the course of evolution? In the context of the evolutionary process, characters are historical individuals, such as species and clades, which have a definite beginning and potentially an end. Since characters are expected to be conservative with respect to certain properties, how did these conservative properties come into existence? This question is called the innovation problem in evolutionary biology (Müller and Wagner, 1991). Arguably this is the most challenging and exciting problem in the evolutionary biology of characters (see the contributions in Section V of this volume). Of course, the complement to the innovation problem is why and how a character may get lost in evolution, a process called reduction. This latter process is usually associated with the loss of function and the accumulation of deleterious mutations, and/or active selection against the functionless character.

I expect that these three questions, or some transformations of them, will be part of any research program that has the character concept at its center. The three areas are very similar to the three ideas that made the species concept a fertile ground for empirical and theoretical research. The modern species concept has its root in the recognition that species are the population biological units of evolutionary change (= explanatory role). They maintain their integrity through isolation mechanisms (= explanation of causal homeostasis). Finally, species originate because of the evolution of isolation mechanisms (= explanation of historical origin). It seems to me that the same conceptual outline, which made the species concept a scientific concept, may help transform the opaque notion of a character into a heuristically productive scientific concept.

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HISTORICAL ROOTS OF THE CHARACTER CONCEPT

Scientific concepts result either from a transformation of a prescientific notion or idea or from the transformation of another scientific concept. Just as organisms are the result of a historical process of modification, concepts and theories are historical entities. This is both an advantage as well as a constraint. The trans-generational history of ideas allows the accumulation of experiences of many lifetimes and thus can lead to greater intellectual depth than the ideas of any individual might have. On the other hand, the history of a concept can constrain or at least bias the directions of thought in ways not entirely justified by empirical facts. The historicity of scientific concepts is largely irrelevant for daily scientific practice, but is highly relevant if we are dealing with the development of new concepts. One has to understand what the objectives were that led past generations to develop a concept in the way as they did. It is also useful to know which avenues of thought have been tried in the past and why they failed to make informed choices in the development of new concepts. It is