Function, Homology, and Character Individuation*

Paul E. Griffiths†

I defend the view that many biological categories are defined by homology against a series of arguments designed to show that all biological categories are defined, at least in part, by selected function. I show that categories of homology are 'abnormality inclusive'—something often alleged to be unique to selected function categories. I show that classifications by selected function are logically dependent on classifications by homology, but not vice-versa. Finally, I reject the view that biologists must use considerations of selected function to abstract away from variation and pathology to form a canonical description of a class of biological systems.

1. Introduction. Over the past quarter of a century a notion of function defined in terms of natural selection has become one of the basic tools of analytic philosophy. Philosophers with no other interest in the biological sciences reach for the 'etiological theory of function' (Millikan 1984, 1993; Neander 1991a, 1991b) whenever they feel the need to distinguish between what merely happens and what is *supposed* to happen. The etiological theory embodies the standard neo-Darwinian view that biological teleology was rendered scientifically respectable by the theory of natural selection:[1]

> If we ask 'What does a cat have sharp, curved claws for?' and answer simply 'To catch mice with', this does not imply a profession of any mythical teleology, but the plain statement that catching mice is the function whose survival value, by the process of natural selection, has bred cats with this particular form of claw. Unless selection is

*Received August 2005; revised March 2006.

†To contact the author, please write to: University of Queensland, School of History, Philosophy, Religion, and Classics, St. Lucia, QLD 4072, Australia; e-mail: paul.griffiths@uq.edu.au.

1. The locus classicus is Pittendrigh (1958, 191–193). Important philosophical discussions include Wimsatt (1972, see especially 70) and Brandon (1981).

Philosophy of Science, 73 (January 2006) pp. 1–25. 0031-8248/2006/7301-0001$10.00
Copyright 2006 by the Philosophy of Science Association. All rights reserved.

https://doi.org/10.1086/510172 Published online by Cambridge University Press

> at work, the question 'What for?' cannot receive an answer with any real meaning. (Konrad Lorenz 1966, 9)

The English word 'function' has many different senses. Two of these seem particularly prominent in the biosciences (Godfrey-Smith 1994; Griffiths 1994):

- Selected function—e.g., a sequence of nucleotides GAU has the selected function of coding for aspartic acid if one reason that sequence evolved by natural selection was because it had the effect of inserting that amino acid into some polypeptide in ancestral organisms.
- Causal function—e.g., a sequence of nucleotides GAU has the causal function of coding for aspartic acid if that sequence has the effect of inserting that amino acid into some polypeptide in the organism in which it occurs.

The idea of causal function (Cummins 1975) is sometimes presented as a rival to the etiological theory of function (Davies 2001). However, both notions are needed to capture the conventional, neo-Darwinian understanding of evolution by natural selection. Neo-Darwinism distinguishes *adaptations*, which have evolved by natural selection, from *adaptive traits*, which increase the fitness of organisms that possess them relative to other types. By definition, every adaptation must at one time have been an adaptive trait, but not all adaptations are still adaptive traits, and not every adaptive trait is yet an adaptation. Translating this into the language of functions, a trait is an *adaptation* for functions which were causal functions contributing to fitness in ancestors, and so became selected functions. A trait is *adaptive* in virtue of some of its causal functions. I say 'some' because the notion of causal function is very liberal. The causal functions which are of primary interest to biologists are those which contribute to an organism's capacity to survive and reproduce (although a pathologist may also be interested in the contributions that specific traits make to disease processes).

Despite the consensus that both notions of function play a role in biology, there is considerable dispute about the specifics of those roles. In particular, there is disagreement as to which notion of function predominates in 'experimental biology' (Weber 2004)—disciplines such as anatomy, physiology, developmental biology, and molecular biology, which experimentally investigate the structure and function of biological systems (Godfrey-Smith 1994; Lewens 2004; Wouters 1995, 2005a, 2005b; Neander 2002; Millikan 2002). In this paper I focus on what I believe is the most influential argument for the view that these sciences investigate selected, as opposed to causal function. The argument is simply that selected function is the means by which biologists *define* the parts and

https://doi.org/10.1086/510172 Published online by Cambridge University Press

processes of the organisms they study. It has become widely accepted in philosophy that biological categories of part and process are defined by their selected function. The claim that hearts are organs whose selected function is to pump blood is commonly taken as an epitome of anatomical classification. This picture of biological categories underlies much of the influential work of Ruth Millikan (1984, 1993, 2002), but it is Karen Neander who has defended the picture most explicitly (Neander 1983, 1991a, 1991b, 2002). It is also Neander who has developed criticisms, based on this view of biological classification, of what she terms 'functional minimalism'—the view, defended by Ronald Amundson and George Lauder and myself, that disciplines like anatomy, physiology, molecular biology and developmental biology individuate characters by homology (Amundson and Lauder 1994; Griffiths 1994): "Bones in the tetrapod limb are classified as carpals because they derive from a particular element in an ancestral tetrapod limb, not because they play the same ecological role" (Griffiths 1996a, S4).

Neander's term 'functional minimalism' is not a happy one for the views of Amundson and Lauder and myself. We assign classification by *causal* function a greater role than Neander herself does. Moreover, on this supposedly 'minimalist' view, classification by selected function also plays a major role in the biological sciences. There are two fundamental aspects to the evolutionary process: heredity and selection. These give rise to two overlaid patterns in the distribution of biological characters, one captured by phylogeny and homology, the other by selected functional classifications (Griffiths 1994, 1996a, 1996b, 1997). Evolution is a matter of 'genealogical actors playing ecological roles' (Hull 1987). Classification by genealogy is seen in modern, phylogenetic systematics, and in the use of homology in sciences such as anatomy, physiology, and comparative morphology. But the same organisms and parts of organisms are classified in terms of their ecological role: organisms are classified into ecological categories like predator and prey, and parts are classified by the ends for which they are adaptations—their selected functions. Neander regards this picture of the role of selected function as 'minimalist' only because she thinks that *all* biological categories are at least partly defined by selected function. Amundson and Lauder and I maintain that unless anatomy, physiology, molecular biology, developmental biology, and so forth turn their attention to specifically evolutionary questions, they investigate function in the causal sense.[2] Neander (2002) replies that the biosciences are always, at least implicitly, investigating function in the selected sense.

2. This claim has also been ably defended by Arno Wouters (1995, 2005a, 2005b).

https://doi.org/10.1086/510172 Published online by Cambridge University Press

I will refer to Neander's thesis as 'functional revanchism', by analogy with the 'revanchist' desire of an empire to regain lost territory.

The dispute between Neander and myself turns primarily on the nature of biological 'characters'. A character is a unit of biological analysis—a part of an organism or a process going on in an organism. Like many other key theoretical terms it is used in a number of not necessarily consistent ways, and has been subject to repeated terminological disputes and attempts at clarification (Wagner 2001; Freudenstein 2005). It is used to refer both to actual parts and processes, and to the property of having a certain part or process, or having it in some specific form. Many authors, particularly in systematics, use 'character' simpliciter to refer to a determinable property (eye color, a genetic locus) while using 'character state' to refer to a determinate value of that determinable (blue, AAATCG). A series of character state changes of the same character is a 'transformation series' for that character. But other authors reject this usage (for a review, see Freudenstein 2005). Finally, like the word 'property' in philosophy, 'character' is used both loosely, to refer to any measurable feature of an organism, and strictly, to refer only to the features recognized by some theory of biological characters: "Although a character is any trait or feature of the phenotype, there are many definitions of 'character', and there has been even more discussion of characters and the character concept" (Hall 2003, 415).

Biological discussion of the character concept proceeds against a general background assumption that characters are 'homologies' in one of the senses discussed below: they are individuated by common ancestry or common developmental mechanisms.[3] This is in stark contrast to the view that biological categories of part and process are defined by their selected function. Once the role of homology in classification is understood, it becomes clear that the picture offered by Neander and Millikan, and widely accepted within philosophy, is fundamentally mistaken. The categories with which 'experimental biology' (Weber 2004) describes structure and causal function are not implicitly teleological, and such straightforward descriptive biology is a necessary basis for making claims about selected function.

In contrast to the mass of philosophical work on selected function,[4] there has until recently been little philosophical work on homology (but see Matthen 1998, 2000; Lewens 2004). In my own earlier work, homology is treated as a concept rooted in phylogenetic systematics. Recently, how-

3. Important recent collections on homology and the character concept include Hall 1994, 1999; Schlosser and Wagner 2004; Wagner 2001; Müller and Newman 2003.

4. Important recent collections on function include Allen, Bekoff, and Lauder 1997; Buller 1999; Ariew, Cummins, and Perlman 2002.

https://doi.org/10.1086/510172 Published online by Cambridge University Press

ever, philosophers of biology have turned their attention to evolutionary developmental biology, a field that has generated an extremely sophisticated theoretical discourse around the concepts of homology, modularity, and character. Philosophers have responded to, and indeed taken part in, this discussion (see Love 2001, 2004; Love and Raff 2003; Raff and Love 2004; Brigandt 2002, 2003a; Winther 2001, forthcoming). Before responding to functional revanchism in more detail, I need to lay out the basic considerations about homology derived from this literature which will underpin my discussion. These considerations apply equally to homologies of structure and to homologies of (causal) function, the importance of which has been evident at least since the rise of modern, Darwinian approaches to behavior.

2. Homology.

> Homologue . . . The same organ in different animals under every variety of form and function. (Owen 1843, 374)

Homology is a relation of biological 'sameness' (Camardi 2001; Brigandt 2002). Here I lay out three fundamentals about homology in contemporary biology: homology is a relation that defines a hierarchy of sets of characters; homologies can be identified at different levels of biological organization; and there are numerous theoretical elucidations of homology, whose relation to the phenomenon of homology is analogous to the relation of the many so-called 'species concepts' to the phenomenon of biodiversity.

2.1. Homology Defines a Hierarchy of Sets of Characters. Like biological taxa, the homologous parts of organisms form groups within groups. The wing of a European house sparrow is homologous to the wing of a flamingo—both are avian wings. The avian wing is homologous to the forelimb of a lizard—both are tetrapod forelimbs. The tetrapod forelimb is homologous to the pectoral fin of a sarcopterygian fish—both are instances of the anterior paired appendages of Sarcopterygii. None of these relationships is a matter of degree—the avian wing is not more or less a homologue of the pectoral fin any more than the class Aves is more or less part of the Sarcopterygii or a sparrow more or less a bird. The scientific practice of identifying biological taxa and that of identifying homologies both originated from the realization that apparently very different organisms or parts of organisms may in fact be modified instances of the same thing, with the result that general knowledge about the more inclusive kind can be sought using the less inclusive kinds as instances. The primary epistemic role of homology is thus that it allows biologists to

https://doi.org/10.1086/510172 Published online by Cambridge University Press

generalize in a principled way across apparently different characters. For example, in the 1830s Johannes Müller clarified the role of the Wolffian body in the development of the human urinogenital system using the organisms which gave the best experimental access to each stage of the developmental sequence, including salamanders, frogs, and birds. He could do this because he was confident that he was studying the same organ in each organism. Conversely, Heinrich Rathke demonstrated that although the hyoid bone is a modified form of the ventral portions of a gill arch, the other identities that had been proposed between the gill arches and structures in the mammalian neck were false, thus invalidating the theories that relied on those identities. It was from this research tradition that biology derived the concept of homology.

Neander writes that "Homology is a relation of degree, somewhat akin to the relation of resemblance or genetic relatedness" (2002, 402), and concludes that when characters are classified by homology, they will form a continuum, something which becomes a key premises in her arguments for functional revanchism. But this is to misunderstand both the nature and function of classifications by homology. The fact that characters can be more or less closely homologous does not mean that they form a continuum, any more than the fact that species can be more or less closely related means that species form a continuum. Explaining this point for species will make it easier to grasp the analogous point for homology. The claim that two species are 'closely related' does not refer to the distance between them on some continuous scale such as Nei's genetic identity.[5] Instead, it refers to the 'taxonomic distance' between them, which is a measure on the topology of a cladogram (Figure 1) or of a phylogenetic tree. One crude measure of taxonomic distance would be to count the number of nodes separating the two species. These nodes represent speciation events, in which what was previously one evolving lineage became two. On some (but not all) views of speciation there may be individuals who are not clearly members of either the parent species or one descendant species. But even on views of speciation which allow this, it does not imply that the descendant species are replaced by a continuum that can only arbitrarily be divided into distinct species. The nodes represent lineage separations and the descendant species we compare do not blend continuously into one another, despite the fact that they evolved gradually from a common ancestor. 'Relatedness' in the taxonomic sense is thus something very different from a measure of similarity.

5. Nei's genetic identity is an overall measure of genetic similarity, usually taken to estimate the proportion of codon differences. By 'genetic resemblance' Neander presumably means either this or Hamilton's coefficient of relatedness, which is the probability that the alleles at some locus in two individuals will be identical by descent.

https://doi.org/10.1086/510172 Published online by Cambridge University Press

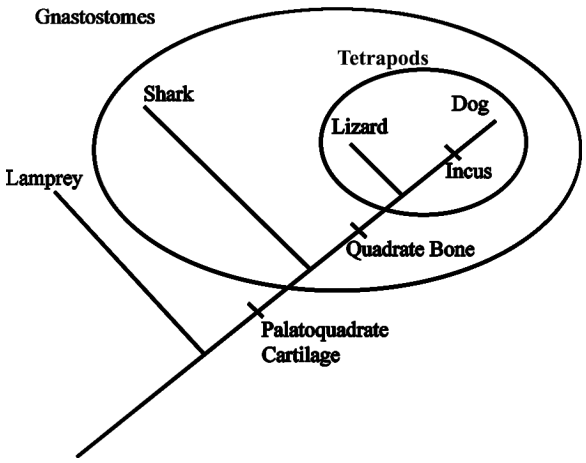


Figure 1. Homologies of the mammalian incus.

In the same way, the claim that two characters are closely homologous means that they are members of a less inclusive, as opposed to a more inclusive, set of modified instances of a single character. The successive modifications of a character that make up a transformation sequence give a classification by homology the same, tree-like, hierarchical character as a cladogram (Figure 1). There are character state changes on the branch at the root of each proper segment of the cladogram, and the character states we compare do not blend continuously into one another, despite the fact that they are modifications of the same ancestral character state. In effect, Neander has rediscovered for homology the old 'chronospecies' problem for systematics—the problem of how to define species using only time-slices of a single, evolving metapopulation (George 1956). Just as the chronospecies problem is a good reason not to define a species by a certain quantity of change in a single, evolving metapopulation, Neander's 'chronotrait' problem is a good reason not to confound homology with something like a measure of morphological similarity.

There may be characters whose homology is uncertain, either for epistemic reasons or for more substantial biological reasons. This is not more puzzling than the fact that the relationships of some taxa are obscure due to lack of evidence or lateral gene-transfer. Some biologists talk of 'partial homology' when the embryonic primordia that typically give rise to two different parts of a organism fuse to form a single part during the ontogeny of an atypical species (e.g., Sattler 1990). Others speaks of 'partial homology' when large characters in different species can be analyzed into smaller characters only some of which are homologous. For example,

https://doi.org/10.1086/510172 Published online by Cambridge University Press

some but not all regions of chromosome 2 in the D genome of hexaploid wheat are homologous to rice chromosome 4 (Gale and Devos 1998). Others speak of 'partial homology' when two parts in different species share developmental mechanisms that are homologous (see next section). But none of these phenomena implies that when characters are classified by homology they form a continuum. Neander does not mention any partial homology phenomena, and it is more likely that she was misled by the non-standard usage of the word 'homology' by some molecular biologists to mean simple physical resemblance between aligned sequences of protein or nucleic acid (Hillis 1999; and see Section 2.4, below).

2.2. Levels of Homology. One of the most exciting developments of the last decade has been the realization that the identity of parts at one level of biological organization may be independent of the identity of their constituent parts at a lower level of organization:

> Both homology and homoplasy can be defined at different levels without making judgments about homology or homoplasy, or lack of homology/homoplasy at other levels. Indeed, to identify the hierarchical level of homology or homoplasy being specified, we should always speak of 'homologous as limbs, homologous as digits, homologous as a developmental process, homologous as a gene network, etc.', and ditto for 'homoplastic as . . .'. (Hall 2003, 425; see also Wagner 2001; Müller and Wagner 1996; Abouheif et al. 1997)

This realization came about primarily as a result of the discovery of highly conserved gene control circuits underlying traits that are not considered to be homologous in themselves. Thus, for example, the paired appendages of vertebrates and arthropods share ancient genetic mechanisms that are hypothesized to have been in place controlling outgrowths of some sort from the bodies of the most ancient animals, and hence are homologous to one another (Shubin, Tabin, and Carroll 1997). Similarly, the vertebrate 'camera' eye and the insect compound eye share genetic mechanisms that may have been involved in the induction of a light-sensitive epithelium prior to the evolution of either eye (Wagner 2001, 5). Nevertheless, neither arthropod and vertebrate paired appendages nor camera and compound eyes are homologous as morphological structures. Conversely, the fact that the gene *bicoid* controls the formation of the anterior-posterior axis in *Drosophila* but not in other dipteran species does not undermine the claim that the elements that form along that axis in *Drosophila* (and indeed the axis itself) are homologous to those in other insects (Laublicher and Wagner 2001, 65–66). Closer to home, the cascade of gene expression that induces masculinization of the fetus in *Ellobius* rodents and the male sexual characteristics that result from that process

https://doi.org/10.1086/510172 Published online by Cambridge University Press

are homologous to those seen in other mammalian species, despite the fact that some *Ellobius* species have lost the Y chromosome and SRY, the 'sex determining' gene (Just et al. 1995). The lesson of these examples is that evolution can preserve a morphological structure while transforming the molecular mechanism that produces it and, conversely, evolution can redeploy an existing mechanism to underpin the development of an evolutionary novelty. Arguably, behavioral homologies and homologies of function in anatomy can form another independent level of homology, with the anatomical structures that support function being transformed over time while the behavioral character or the functional character (e.g., the biomechanical profile of a movement) remains the same (Lauder 1990). Levels of biological organization are not completely independent, of course. Homology of underlying mechanisms is important, but not indefeasible, evidence for homology at a higher level.

2.3. 'Homology Concepts'. As with the species concept, there are alternative theoretical elucidations of homology, which biologists refer to as different 'homology concepts' and often think of as competitors. Here I can only sketch the two main approaches (for more detail see Brigandt 2002, 2003a; Hall 1994, 1999, 2003; Wagner 2001). 'Taxic' or 'Darwinian' approaches to homology treat characters in two or more organisms as homologous if they are descended from a single character in an ancestral organism. 'Developmental' or 'biological' (Wagner 1989) approaches, however, treat characters as homologous if the preferred theory of how organisms develop identifies them as instances of the same developmental phenomenon at some level of analysis (see above). Günter Wagner has argued that the taxic approach is essentially parasitic on a developmental understanding of homology, because it defines character identity horizontally—between taxa—but not vertically—between parent and offspring. Unlike whole organisms, parts of organisms do not give birth to little parts and so two parts in one organism cannot be literally 'descended from a common ancestral part' (except in the case of parts actually present in the gametes, such as genomes; see Section 2.4). The taxic approach thus presupposes and leaves unanalyzed the claim that certain characters in offspring are the same as (homologous to) certain characters in their parents. At the level of biological practice, this need not be a serious problem. Different homology concepts find their homes in different biological disciplines and reflect the particular needs of those disciplines (Brigandt 2002, 2003a). The taxic homology concept finds its home in disciplines concerned with reconstructing evolutionary change, disciplines that are only concerned with homologies between different taxa ('taxic homologies'). These disciplines can begin with a character set consisting of more or less arbitrary, operational, characters, and bootstrap their way

https://doi.org/10.1086/510172 Published online by Cambridge University Press

into a set of characters whose stability and congruence with one another are reason to believe that they represent real morphological units (Griffiths 1999). But at a theoretical level, this procedure works only because there *are* real units of evolutionary change, and the taxic homology concept does nothing to explain this: "the main goal of a biological [*developmental*] homology concept is to explain why certain parts of the body are passed on from generation to generation for millions of years as coherent units of evolutionary change" (Wagner 1994, 279).

The most striking difference between the taxic and developmental approaches is that the former is simply inapplicable to 'serial homology'—the homology relationship that holds between different vertebrae in the spine or different segments in an arthropod. Serial homologues are repeated parts of a single organism, rather than corresponding parts on different organisms, as the taxic approach requires. One appealing but ultimately uninformative way to deal with serial homology is to say that both taxic and serial homology occur when two characters 'share genetic information'. This proposed solution can also be extended to answer Wagner's criticism of the taxic homology concept—the homologous characters of offspring and parent occurs are those which 'share genetic information'. But 'shared genetic information' here has two possible interpretations. On one interpretation the proposed definition does not work, and on the other it collapses into the developmental homology concept. The first interpretation takes 'genetic information' to be the sequence information (sensu Crick) located in DNA elements. The discussion of levels of homology above shows that homology defined as shared genetic information in this sense will yield the wrong answer in many cases (Roth 1999, 321–324; Abouheif et al. 1997). Shared genetic information in this sense is, like shared embryonic origin, good but defeasible evidence for homology. The second interpretation takes 'genetic information' to be developmental information in some more general sense—whatever it is in the developmental matrix that allows organisms to reliably reconstruct form across the generations. For example, 'genetic information' in this sense may turn out to be an emergent and multiply realizable property of genomic regulatory networks. But rather than clarifying the homology concept, the appeal to genetic information in this sense is no more than a promissory note for a developmental homology concept. The idea that homologues reflect shared 'genetic information' becomes another way to state that characters are homologous if they are instances of the same phenomenon at some level of analysis in a theory of how organisms develop.

What then is homology? It is a manifest fact that the same parts and processes can be found in different organisms and in different places in one organism, just as it is a manifest fact that organisms form species.

https://doi.org/10.1086/510172 Published online by Cambridge University Press

Both ideas could be wrong, but the burden of proof is massively on the side of the sceptic. In the early nineteenth century, biologists started to develop powerful operational methods for identifying these parts and processes and that research tradition has ever since provided the basis for the investigation of structure and (causal) function—'the hierarchical basis of comparative biology' (Hall 1994). So homology, like the existence of species, is a phenomenon that stands in need of explanation (Brigandt 2003b). It has been clear since Darwin that a critical part of that explanation is provided by common descent. However, the criteria of homology have in each period reflected the contemporary understanding of how organisms grow, and it is clear that developmental biology is another critical component of the explanation. As everywhere in science, our understanding of the phenomenon of homology gets refined by our attempts to explain it.

2.4. Homology in Molecular Biology. Some molecular biologists use the term 'homology' to refer to the degree of correspondence between aligned sequences of nucleic acid or protein. Thus, they might describe two genes as 50% homologous or as having 50% 'sequence homology' (Hillis 1999). 'Homology' in this usage is best regarded not as an alternative theoretical interpretation of homology, but merely as a homonym (Brigandt 2003a). In support of this interpretation, note that molecular biologists have invented a new term for homology in the traditional sense, or, in fact, two new terms. Nucleic acid sequences, proteins, etc., which are shared by different species as a result of descent from a single ancestral species are called 'orthologues' (taxic homology). Genes in the same genome originating from gene duplication events are called 'paralogues' (serial homology). In addition, sequences which enter one genome from another genome by lateral transfer are known as 'xenologues'. The use of 'homology' to refer to mere sequence similarity of molecules still raises the hackles of many biologists, including many molecular biologists, so in the rest of this paper I will stick to the traditional usage.

3. Neander on Taxic Homology. Neander (2002) is highly critical of my claim that "A homologous trait is a character that unites a clade. Every species in the clade either has the trait or is descended from a species that has it" (Griffiths 1994, 212; see also Amundson and Lauder 1994, 454). A clade is a taxon which contains an ancestral species and all its descendant species, and this was an attempt to capture the notion of taxic homology, which I then referred to as 'cladistic homology'. My definition is inadequate because it takes no account of the alternative approaches to homology described above, and because it does not mark the distinction

https://doi.org/10.1086/510172 Published online by Cambridge University Press

between primitive and derived characters, both of which may 'unite' a clade in the sense specified. But these are not Neander's criticisms.

Neander derives numerous absurdities from my definition. She interprets that definition to mean not just that some biological characters unite certain clades, but also that those characters have *no other properties of any kind*. This allows her to argue that on my definition we cannot distinguish a species that actually has a homologous trait from a species which has lost the homologous character through evolution. Furthermore, we cannot distinguish two characters shared by the same clade, and we cannot identify the point in an evolutionary tree at which the character first occurs, because we can say nothing about it except that it first occurs at that point. Neander also suggests that because all organisms are descended from a single common ancestor, my definition collapses all traits to 'The Trait', but this particular criticism seems to rest on her mistaken view that the homology relation behaves formally like a measure of overall similarity. The rest of Neander's criticisms come to this: ". . . before two traits can be identified as homologous with respect to each other, we need some *specification of the traits* in question" (Neander 2002, 402). But the 'character' referred to in my definition is just this 'specification of the traits in question'. The definition was intended to characterize homology as understood in cladistic systematics, and it should be read in line with the basic cladistic procedures described in Griffiths (1994). In cladistics, homologies are inferred from a set of measured similarities between organisms, known as 'shared characters'. Suppose we want to construct a cladogram using sequence data from a suitable molecule, such as 28S ribosomal RNA. The aligned sequences from any two species will be identical at some positions and different at others. Where they are identical, this shared character may be a homology or it may be a homoplasy, depending on whether the nearest common ancestor of the pair had this character state and whether there have been any intervening character state changes in either lineage. Hence when we say that the character state of the first nucleotide in each sequence is C we are giving a physical specification—that nucleotide is cytosine. After constructing the cladogram which our preferred algorithm identifies as the best explanation of the whole pattern of similarity and difference amongst the sequences, we may conclude that having C at that position is a homologue uniting some clade of the organisms we are classifying. But some species in the clade may *not* have C at that position if the simplest explanation of the whole pattern of data is that this particular species has lost C. Conversely, some species outside the clade may have acquired C by convergent evolution. Those species have the same character state, but in their case it is not an example of the homologue we have identified.

It is genuinely confusing that 'character' can mean either any measur-

https://doi.org/10.1086/510172 Published online by Cambridge University Press

able property of an organism or only a property recognized as biologically meaningful in some theory of the organism. However, philosophers are familiar with just the same ambiguity in the term 'property' itself, which can be used loosely to refer to any definable characteristic or more strictly to refer only to those 'properties' recognized in some philosopher's ontology. Griffiths (1994) was a discussion of cladistic approaches to homology, so a charitable reading would take 'character' in my definition to have the sense it has at the corresponding point in the cladistic procedure for inferring homology—a measurable point of resemblance between taxa that may or may not be a 'real' resemblance (a homology). Characters like flight and the 'camera' eye, which I discussed, make it clear how cladistic systematists avoid the absurdities that Neander identifies. The 'camera' eye is shared by vertebrates and cephalopods but is not homologous in these two taxa. It is perfectly consistent to define the *vertebrate eye* as a certain kind of structure (the camera eye) when and only when that structure appears in a particular clade of organisms (the vertebrates). Some subterranean vertebrates have lost their eyes and the camera eye character evolved independently in some ancestral cephalopods.

4. Revanchism I: 'Functional Homologues'. Neander offers three arguments for functional revanchism. The final one is her master argument, designed to show that all descriptions of structure or causal function in biology depend on prior knowledge of the selected function of the relevant characters. It is clear from her presentation, however, that the other two arguments are supposed to have some independent force, so I will consider them before proceeding to the master argument.

Neander's first argument is that if biologists are to establish any clear distinction between one part and another, they must of necessity supplement considerations of homology with considerations of selected function. Consequently, the parts of organisms are what she calls 'functional homologues'. Now, 'functional homologues' in molecular biology are molecules that play the same causal role (Abouheif et al. 1997), and 'homologies of function' in morphology are causal functions which two species can perform because a common ancestor performed them, but Neander is not using 'functional homologue' in either of these existing senses. Instead, she uses the phrase to refer to taxic homologues which stand out in a transformation sequence because they introduce a novel functional role—something closer to what biologists call 'key innovations'. She writes:

> If we conceive of the phylogenetic tree as a branching flow of (genetic and other) information, the issue is how to draw a conceptual line in this flow. Clearly there will be few if any sharp boundaries. None-

https://doi.org/10.1086/510172 Published online by Cambridge University Press

> theless, we must distinguish one trait from another, for physiology requires such distinctions. My suggestion, the central suggestion of this chapter, is this: One main way in which this is done is by drawing conceptual lines at those places where there is a significant change in what there was selection for. (Neander 2002, 403)

The picture Neander seems to have in mind is that of a paleontologist following the transformation of, say, a lobe-fin into a tetrapod limb and being unable to say in exactly which ancestor the transition from fin to limb occurred. This picture is consistent with her belief that classifying characters by homology involves placing them at points along a continuum. This picture has been criticized above (Section 2.1). Classification by homology involves placing morphologically distinct characters on a tree, thus establishing one or more transformation series and revealing what were previously seen as distinct characters as different states of a single character.[6] But it may be a mistake to take Neander at her word when she says that homologues grade indistinguishably into one another. We can read her as a traditional Darwinian gradualist who believes that there is a vast hierarchy of homologies within homologies, each representing a tiny character state change, and that the problem is to single out some of these changes as significant. It not really that there are 'few if any sharp boundaries' but rather that there are too many, insignificant boundaries. On this reading she is discussing the problem of 'evolutionary novelty' (Mayr 1960). I will interpret Neander in this way and show that in her own chosen example it is simply not true that the prominent stages in the transformation sequence are defined by changes in the selection pressures acting on the character.

The most detailed example Neander gives of how adaptive function can supplement a classification by homology concerns "the mammalian inner ear bones and the reptilian jaw bones and the portions of the gill arches of fishes that are their homologues" (Neander 2002, 402). What she has in mind is that one of the mammalian middle ear ossicles, the incus, is homologous with the quadrate bone in the clade containing all terrestrial vertebrates and the bony fishes (osteichtyans). This character in osteichtyans is homologous with the palatoquadrate cartilage, part of the mandibular arch (jaw) in sharks and rays, and this character in gnathostomes, the clade of jawed vertebrates, is homologous with the first

6. An anonymous referee has helpfully remarked, "Names like 'incus' and 'quadrate', 'malleus' and 'articulate', and 'stapes', 'columnella' and 'hyomandibular' were in use long before it was known that they were homologous. So, historically speaking, the problem is one of establishing homologies between structures that are distinguished on the basis of traditional morphological criteria rather than of drawing conceptual lines within a group of known homologies."

https://doi.org/10.1086/510172 Published online by Cambridge University Press

gill-arch in jawless fish, such as the lamprey (Figure 1). It is plausible that these distinct characters were linked by many intermediates and Neander claims that biologists divide the series into a small number of named characters because they "[draw] conceptual lines at those places where there is a significant change in what there was selection for (for example, from selection for jaw support to selection for audition)" (Neander 2002, 403). Her suggestion is that the transformation series should be divided into three segments (gill arch, jaw bones, ear bones) rather than two or four because there are two distinct changes of selected function, from breathing to jaw support and from jaw support to hearing. But, first, this is certainly not the only way in which biologists single out character state changes as particularly significant, and, second, when biologists do treat a character state change as a 'key innovation' this is not because they need to draw a line in a bafflingly complex transformation series.

The transformation series chosen by Neander consists of at least four characters, although it is often useful to distinguish more, for example distinguishing the state of the quadrate bone in modern bony fishes from its state in terrestrial vertebrates. The most basic set of distinctions is that between incus, quadrate bone, palatoquadrate cartilage, and gill arch. Two of these, the quadrate bone and palatoquadrate cartilage, could be described as functioning in 'jaw support'. The prominence of these four stems from the fact that they are the actual character states seen in a nested set of major taxa: jawless fishes, cartilaginous fishes, bony fishes (including non-mammalian terrestrial vertebrates), and mammals (Figure 1). The fact that the four are not defined by their selected function in the way Neander suggests is evident from the usual theories about their evolution. It is not true that the quadrate bone functions in jaw support, whereas the incus functions in hearing. In lizards the quadrate bone plays a critical role in hearing. It transmits vibration from the ground—something with obvious adaptive significance for both predator and prey. In snakes it also transmits vibrations from the air, via a portion of the skin. The transformation of the quadrate into the incus may have been driven by increased selection for hearing in early, nocturnal mammals, but what creates an obvious break at this point in the series is not a change of function but traditional morphological criteria—the quadrate bones in all the other osteichtyans have no obvious resemblance to the incus that we see in mammals. The realization that the incus is a modified quadrate was the result of comparative anatomists looking for a way to bring their descriptions of many different vertebrate skeletons under a single, general account of the structure of the vertebrate skeleton. Turning to the other character that Neander claims is defined by a selected function, recent research suggests that the initial evolution of the vertebrate jaw—the enlargement and more powerful articulation of the first gill arch to allow

https://doi.org/10.1086/510172 Published online by Cambridge University Press

it to close the mouth cavity—was an adaptation to move water through the gills and was only later co-opted for feeding (Mallatt 1996). Thus, while 'jaw' is plausibly a functional term, like 'wing', the vertebrate jaw itself is not defined by its function, but is a homologue identified using traditional morphological characters, both structural and (causal) functional (e.g., enlargement and more powerful articulation).

Neander's 'functional homologues' resemble what biologists call 'key innovations'—features like the vertebrate jaw which make it possible for an organism to perform a new adaptive function and may underpin an adaptive radiation by its descendants (Mayr 1960). In modern synthesis biology, with its strong emphasis on gradual change, this idea was used to make sense of the idea of evolutionary novelty: novelties are character state changes which enable new functions. However, this notion was not introduced to draw distinctions in bafflingly continuous transformation series, but to elucidate the idea that some new characters are genuinely novel, while other are merely variations on a theme. Moreover, recent work on evolutionary novelty has focused on a different elucidation of this idea: a novelty is a character that cannot be homologized to any preexisting character, such as the Chelonian (turtle) shell (Müller and Wagner 1991; for philosophical discussion, see Love 2001, 2004). So while some homologues may be prominent because their appearance marks the ability to perform a new function (first as causal, then as selected), others are prominent because their appearance marks the beginning of a new structure.

In conclusion, then, Neander has mischaracterized the scientific problem that the concept of homology is used to solve. The problem is one of identifying correspondences between characters in different taxa, characters that have already been independently described. This problem remains the same when the homologous structures are being identified in fossils with the aim of reconstructing the course of evolution. Even when biologists do confront the problem of singling out the most significant character state changes in a transformation sequence, as when they try to single out 'novelties' from less significant changes, they do so by identifying structural innovations as well as functional innovations.

5. Revanchism II: The Appeal to Practice. Before offering her 'master argument', Neander makes a straightforward appeal to biological practice. She points out that biologists study the function, as well as the structure, of the parts of organisms and offers an example in which physiologists have classified muscle fibers using a functional property, namely the manner in which they contract (2002, 408). She says that systematists sometimes look at these functional properties when making homology judgments (409). The problem with this appeal to practice is that it equivocates

https://doi.org/10.1086/510172 Published online by Cambridge University Press

on two sense of the word 'function'. Descriptive functional properties (e.g., actual causal roles) play a critical role in anatomical and physiological reasoning. But descriptive functional properties, such as the biomechanical properties of the jaw, or units of animal behavior, such as the 'ghost dive' and the 'weed trick' in the famous courtship display of the great crested grebe (Huxley 1914), are on a par with descriptive structural properties like bone density or feather morphology. These descriptive properties, whether functional or structural, are the things that are judged homologous or analogous between species. The relative importance of descriptions of causal function and descriptions of structure in anatomy and physiology is a completely separate issue from the relative importance of selected function and homology.

There is a sense in which this reply is unfair to Neander, since she believes that all references to function (and indeed structure) are implicitly references to adaptive function. But unless that 'master argument' succeeds, her appeal to biological practice simply fails to mark the distinction between what something actually does and what natural selection has designed it to do. Moreover, not marking this distinction causes her to misunderstand Amundson and Lauder (1994). Neander argues that their account reduces to the view that biological classification is classification by structure alone (2002, 409–410). Even the title of their paper is misleading, she says, because it promises a defense of 'the use of causal role functions in biology' while the paper only defends the use of structural descriptions in biology (Neander 2002, 393). But Lauder is a functional morphologist, and well-known for his advocacy of the importance of functional characters in diagnosing homology. If we consider Neander's own example, muscle contractions, Lauder has written, "I would argue that any definable pattern of muscle movement is an organismal character just like any structural feature. Just like a structural character, functions may be considered homologous if they characterize a natural, monophyletic clade of taxa" (Lauder 1999, 186). The idea that Amundson and Lauder advocate classification by structure alone is quite mistaken. They think anatomical characters are classified by homology in the sense usual in the science of which Lauder is a practitioner and Amundson a historian—a historical relationship diagnosed using evidence from both structural and (causal) functional characters. Neander accuses them of mistaking the structural criteria used to recognize characters for what actually defines those characters (2002, 410). In fact, they use descriptive criteria in just the way she recommends, but to infer homology, not selected function. They make a powerful case that 'functional' anatomy and morphology study causal functions and Neander's appeal to practice does nothing to blunt the force of their argument. It is left to her deeper, philosophical, argument to convince us that when scientists report the

https://doi.org/10.1086/510172 Published online by Cambridge University Press

results of their experimental analyses of anatomical structures they are, implicitly, inferring the selection history of those structures.

6. Revanchism III: Abnormality Inclusive Categories. Neander's argument that all references to function (and indeed structure) in anatomy, physiology, morphology, and similar sciences are implicit references to selection history is a simple one. She notes that the categories used in these sciences include abnormal instances. A heart that cannot pump blood is still a heart; a deformed quadrate bone is still a quadrate bone; and an abnormal 'weed trick' produced by a neurologically impaired grebe is still a 'weed trick'. She argues that 'abnormality inclusive categories' must be 'essentially historical categories' (2002, 413), from which she infers that they must be defined by selected function:

> The relevant notions [of function and structure] are both 'normative' in the sense that they are both notions of the normal, in the teleological as opposed to the statistical sense of the term, if we assume an etiological account of each of them. Abnormality inclusive categories involve a notion of structure and function that is, to recall the title of Amundson and Lauder's paper, with, not without, a purpose. (Neander 2002, 414)

But categories of taxic homology are equally 'essentially historical' and equally able to include abnormal instances. Abnormal and diseased instances of a character are homologous to normal instances because abnormal and diseased instances are descended from the same common ancestor as normal instances. So even if abnormality inclusive categories have to be 'essentially historical' this is no argument against their being defined by homology.

Moreover, abnormality inclusive categories do not have to be 'essentially historical' in Neander's sense. The developmental approach to homology yields abnormality inclusive categories which are not essentially historical. This should come as no surprise: it would be puzzling if an approach designed to identify characters across evolutionary transformations could not identify them across perturbing causes such as disease processes. Thus, for example, my first cervical vertebra is serially homologous to my damaged third lumbar vertebra for the same reason that it is serially homologous to my undamaged fourth lumbar vertebra. All three vertebrae differ in form, but all are instances of a repeated unit of development identified by a theory of the vertebrate skeleton. The development of L3 was a perturbation of *that particular* developmental pattern.

Neander's 'master argument' fails, and the need for abnormality inclusive categories can be met using homology. But this is not to say that

https://doi.org/10.1086/510172 Published online by Cambridge University Press

biology does not use selected function categories. Biological 'analogies' are classifications by shared evolutionary purpose (selected function). They group together homologues in virtue of shared features of their (separate) selection histories. The avian wing is a modified tetrapod forelimb that evolved at a particular point in evolutionary history. So the avian wing is a homology uniting the class Aves. The chiropteran (bat) wing is a tetrapod forelimb modified in a radically different way at a different point in evolutionary history. So the chiropteran wing is a homology uniting the order Chiroptera. Although the wings of birds and bats are homologous as tetrapod forelimbs, they are not homologous as wings. Both sets of modifications to the forelimb, however, are explained to a very significant extent by selection for the ability to fly. So 'wing' is an analogy—a category defined by selected function.

There is, however, a fundamental asymmetry between analogies and homologies. Classifications by selected function (analogies) are logically dependent on classifications by homology (Griffiths 1994, 213–214; see also Neander 2002, 405, note 12; Lewens 2004, 99–100). Consider:

1. A character has a selected function only if it is a member of a lineage of characters that has a history of selection for that function.
2. Organisms give birth to organisms, but characters do not give birth to little characters and so they do not form lineages except as corresponding parts of ancestor and descendant, that is, as homologues.
3. To say that a character token *t* has some selected function is, by definition, to say that *t* is a token of a type *T* defined by homology and there is a lineage of tokens of *T* with a history of selection for that function.

Even a hypothetical assignment of selected function to a character is, by definition, a hypothetical postulation of a series of ancestral characters to which that character is homologous. In contrast, classifications by homology are logically independent of classifications by selected function. The claim that two characters are homologous is quite consistent with neither of the characters having *any* selected function: deleterious mutations found in two different species, for example, can be homologous.

The argument of the last paragraph suggests that the 'etiological theory' of selected function is incomplete in just the same way as the taxic approach to homology (see Section 2.3). Both theories must be supplemented by an account of trans-generational character identity. Millikan recognizes this, which is why her definition of selected function rests on a theory of 'reproductively established families' (Millikan 1984, 19–25). A developmental account of homology, which is what Wagner envisages filling the gap in the taxic account of homology (see Section 2.3), would provide what Millikan calls the 'laws in situ' (e.g., a mechanism for reproduction),

https://doi.org/10.1086/510172 Published online by Cambridge University Press

whose existence is required to make one item a reproduction of another and create a 'first-order reproductively established family' (1984, 20).

7. Selection and Biological Idealization. I have shown that classifications by homology can be 'abnormality inclusive' in at least two different ways. I suspect, however, that many readers will wonder whether this is not merely one aspect of a larger problem that only an appeal to selected function can solve. Biological systems are highly variable, so how can biologists construct a canonical description of a certain *type* of system without relying on a distinction between what is evolutionarily Normal and evolutionarily abNormal (Millikan 1984)—between those features designed by natural selection and those not so designed? In a recent paper, Millikan (2002) has suggested that the Normal/abNormal distinction is needed not just to distinguish normal from pathological variation, but also to identify what is inside and outside a single biological system, and to define the conditions under which that system is *operating* as opposed to participating in biologically irrelevant causal processes such as being dissolved in acid. Millikan's concerns, and similar concerns voiced by Neander, point to an important issue, namely, the nature of scientific idealization in the biological sciences. Darwinian populations are clusters of variation not constrained by any ideal type, but experimental biologists need to construct idealized models of the individuals that make up those populations. The study of how this is accomplished is made more urgent by the emerging consensus that scientific explanation in biology consists to a very considerable extent of the discovery of mechanisms—highly idealized descriptions of the operation of chosen causal pathways through complex biological systems (Craver and Darden 2005). While there is no space here to give a full account of biological idealization (Griffiths, in preparation), I will briefly indicate some resources that are available to experimental biologists in the construction of ideal systems for causal analysis.

First, like scientists in most other fields, biologists construct mathematical models of complex systems, abstracting away from those aspects of the biology that cannot be tractably modelled with the chosen formalism. In this respect, an idealized cell is no different from an idealized model of a subduction zone in geology. The cell is not simplified in the model because evolution designed the cell to be a perfect rectangle and all departures from this form are abNormal. It is simplified for the same reason that the shape of the two plates is simplified in the model of subduction—to reduce the computational complexity of the model.

Second, the purpose of many 'model systems' is to facilitate discovering basic mechanisms. A first step in a discovery process of this kind is the choice—or more likely the construction—of one or more model systems.

https://doi.org/10.1086/510172 Published online by Cambridge University Press

A model system is a practical idealization—an actual physical system competent to produce the effect to be explained and tractable to experiment using the techniques to hand. The final explanation—the mechanism—consists of a description of the actual operation of one or more model systems. When biological idealization takes the form of the construction of a model system for the elucidation of a basic mechanism, the experimenter need not be concerned whether the experimental system is Normal. Because the questions being investigated concern the basic mechanisms that allow certain life processes to occur, it can be assumed that any model system derived from the original in which the effect can be produced will retain these mechanisms.[7] The most important feature of the model system is tractability in the laboratory. Laboratory strains of the nematode worm *C. elegans*, for example, were not bred to be Normal but to be identical and easy to maintain.

Third, in many cases the function of a standardized description of a biological system is to provide a reference standard, so that many researchers can work on identical material, and so that the variation they uncover in natural examples of the system can be characterized against that common standard. 'The human genome' is a good example. Little effort was made to ensure that the material sequenced by either the public or the private project was Normal. The most important feature of the data stored in the human genome reference sequence is that it is readily available to all researchers.

Thus, while there are clearly some contexts in which biologists need to appeal to something like evolutionary Normality in order to characterize an appropriate ideal system for analysis, there are many other contexts in which biologists use other forms of idealization. This should not be surprising, since idealization is a ubiquitous part of scientific discovery and explanation, rather than something confined to those parts of science which study the products of evolution. Ecosystems, for example, are as complex as organisms and examples of any one type of ecosystem vary greatly. Nevertheless, ecologists do not need to appeal to postulate a cosmic selection process in order to construct idealized models of ecological processes.

8. Conclusion. It is agreed on all hands that the etiological theory of function captures the sense of 'function' in which many neo-Darwinians have used the term: the purpose(s) for which a character evolved by natural selection (selected function). However, several authors have main-

7. Wouters makes a similar point when he identifies the target of explanation in much experimental biology as the *viability* of the organism, rather than its ability to produce a selectively optimal phenotype (Wouters 1995, 2005a).

https://doi.org/10.1086/510172 Published online by Cambridge University Press

tained that the sense of 'function' in which biologists have talked for well over a century about 'form and function', and the sense in which experimental sciences such as anatomy, physiology, comparative morphology, developmental and molecular biology experimentally elucidate 'form and function' is causal function (Amundson and Lauder 1994; Amundson 2005; Griffiths 1994; Lewens 2004; Wouters 1995, 2005a, 2005b). Karen Neander has argued that these authors are mistaken on the grounds that the categories of part and process found in these sciences are all at least partially defined in terms of selected function.

In this paper I have shown that the claim that all biological description makes implicit claims about the selective history of the characters described is not supported by Neander's arguments, including the important and influential argument from abnormality inclusive categories. I have argued that classifications by selected function are logically dependent on classifications by homology, but not vice versa. Finally, I have argued that while enthusiasts for selective function have drawn attention to an important topic for future research—the nature of idealization in the biological sciences—their conclusion that idealization is achieved by appealing to selection history is premature.

REFERENCES

Abouheif, Ehab, Michael Akam, William J. Dickinson, Peter W. H. Holland, Axel Meyer, Nipam H. Patel, Rudolf A. Raff, V. Louise Roth, and Gregory A. Wray (1997), "Homology and Developmental Genes", *Trends in Genetics* 13: 432–433.

Allen, C., M. Bekoff, and G. V. Lauder, eds. (1997), *Nature's Purposes: Analyses of Function and Design in Biology*. Cambridge, MA: MIT Press.

Amundson, Ron (2005), *The Changing Rule of the Embryo in Evolutionary Biology: Structure and Synthesis*. New York: Cambridge University Press.

Amundson, Ron, and G. V. Lauder (1994), "Function without Purpose: The Uses of Causal Role Function in Evolutionary Biology", *Biology and Philosophy* 9: 443–470.

Ariew, André, Robert Cummins, and Mark Perlman, eds. (2002), *Functions: New Essays in the Philosophy of Psychology and Biology*. New York: Oxford University Press.

Brandon, R. (1981), "Biological Teleology: Questions and Explanations", *Studies in the History and Philosophy of Science* 12: 91–105.

Brigandt, Ingo (2002), "Homology and the Origin of Correspondence", *Biology and Philosophy* 17: 389–407.

——— (2003a), "Homology in Comparative, Molecular and Evolutionary Biology", *Journal of Experimental Zoology (Molecular and Developmental Evolution)* 299B: 9–17.

——— (2003b), "Species Pluralism Does Not Imply Species Eliminativism", *Philosophy of Science* 70: 1305–1316.

Buller, David J., ed. (1999), *Function, Selection and Design*. Buffalo: SUNY Press.

Camardi, Giovanni (2001), "Richard Owen, Morphology and Evolution", *Journal of the History of Biology* 34: 481–515.

Craver, Carl F., and Lindley Darden (2005), "Special Issue: Mechanisms in Biology", *Studies in History and Philosophy of Biological and Biomedical Sciences* 36: 233–464.

Cummins, Richard (1975), "Functional Analysis", *Journal of Philosophy* 72: 741–765.

Davies, Paul Sheldon (2001), *Norms of Nature: Naturalism and the Nature of Functions*. Cambridge, MA: MIT Press.

https://doi.org/10.1086/510172 Published online by Cambridge University Press

Freudenstein, John V. (2005), "Characters, States, and Homology", *Systematic Biology* 54: 965–973.
Gale, Michael D., and Katrien M. Devos (1998), "Comparative Genetics in the Grasses", *Proceedings of the National Academy of Sciences of the USA* 95: 1971–1974.
George, T. Neville (1956), "Biospecies, Chronospecies and Morphospecies", in P. C. Sylvester-Bradley (ed.), *The Species Concept in Palaeontology*. London: Systematics Association, 123–137.
Godfrey-Smith, Peter (1994), "A Modern History Theory of Functions", *Noûs* 28: 344–362.
Griffiths, Paul E. (1994), "Cladistic Classification and Functional Explanation", *Philosophy of Science* 61: 206–227.
——— (1996a), "Darwinism, Process Structuralism and Natural Kinds", *Philosophy of Science* 63: S1–S9.
——— (1996b), "The Historical Turn in the Study of Adaptation", *British Journal for the Philosophy of Science* 47: 511–532.
——— (1997), *What Emotions Really Are: The Problem of Psychological Categories*. Conceptual Foundations of Science, ed. D. Hull. Chicago: University of Chicago Press.
——— (1999), "Squaring the Circle: Natural Kinds with Historical Essences", in Robert A. Wilson (ed.), *Species: New Interdisciplinary Essays*. Cambridge, MA: MIT Press, 208–228.
——— (in preparation), "'Nothing in Biology Makes Sense Except in the Light of Evolution.' Discuss".
Hall, Brian K., ed. (1994), *Homology: The Hierarchical Basis of Comparative Biology*. New York: Academic Press.
———, ed. (1999), *Homology*. Novartis Foundation Symposia, ed. Gregory R. Bock and Gail Cardew, vol. 222. Chichester, UK: John Wiley and Sons.
——— (2003), "Descent with Modification: The Unity Underlying Homology and Homoplasy as Seen Through an Analysis of Development and Evolution", *Biological Review* 78: 409–433.
Hillis, David M. (1999), "Homology in Molecular Biology", in Brian K. Hall (ed.), *Homology: The Hierarchical Basis of Comparative Biology*. San Diego: Academic Press, 339–368.
Hull, David L. (1987), "Genealogical Actors in Ecological Roles", *Biology and Philosophy* 2: 168–184.
Huxley, Julian (1914), "The Courtship-Habits of the Great Crested Grebe (*Podiceps Cristatus*); with an Addition to the Theory of Sexual Selection", *Proceedings of the Zoological Society of London* 35: 491–562.
Just, Walter, Wolfgang Rau, Walther Vogel, Mikhail Akhverdian, Karl Fredga, Jennifer A. Marshall Graves, and Elena Lyapunova (1995), "Absence of Sry in Species of the Vole Ellobius", *Nature Genetics* 11: 117–118.
Laublicher, Manfred D., and Günter P. Wagner (2001), "How Molecular Is Molecular Developmental Biology? A Reply to Alex Rosenberg's Reductionism Redux: Computing the Embryo", *Biology and Philosophy* 16: 53–68.
Lauder, G. V. (1990), "Functional Morphology: Studying Functional Patterns in an Historical Context", *Annual Review of Ecology and Systematics* 21: 317–340.
——— (1999), "Homology, Form and Function", in Brian K. Hall (ed.), *Homology: The Hierachical Basis of Comparative Biology*. New York: Academic Press, 151–196.
Lewens, Tim (2004), *Organisms and Artifacts: Design in Nature and Elsewhere*. Cambridge, MA: MIT Press.
Lorenz, Konrad Z. (1966), *On Aggression*. Translated by Marjorie Kerr Wilson. New York: Harcourt, Brace and World.
Love, Alan (2001), "Evolutionary Morphology, Innovation, and the Synthesis of Evolution and Development", *Biology and Philosophy* 18: 309–345.
——— (2004), "Morphological and Paleontological Perspectives for a History of Evo-Devo", in Jane Maienschein and Manfred D. Laublicher (eds.), *From Embryology to Evo-Devo: A History of Embryology in the 20th Century*. Cambridge, MA: MIT Press.
Love, Alan, and Rudolf A. Raff (2003), "Knowing Your Ancestors: Themes in the History of Evo-Devo", *Evolution and Development* 5: 327–330.

https://doi.org/10.1086/510172 Published online by Cambridge University Press

Mallatt, Jon (1996), "Ventilation and the Origin of Jawed Vertebrates: A New Mouth", *Zoological Journal of the Linnean Society* 117: 329–404.
Matthen, Mohan (1998), "Biological Universals and the Nature of Fear", *Journal of Philosophy* 95: 105–132.
——— (2000), "What Is a Hand? What Is a Mind?" *Revue Internationale de Philosophie* 214: 653–672.
Mayr, Ernst (1960), "The Emergence of Evolutionary Novelties", in *Evolution after Darwin*. Chicago: University of Chicago Press, 349–380.
Millikan, Ruth Garrett (1984), *Language, Thought and Other Biological Categories*. Cambridge, MA: MIT Press.
——— (1993), *White Queen Psychology and Other Essays for Alice*. Cambridge, MA: MIT Press.
——— (2002), "Biofunctions: Two Paradigms", in Robert Cummins, André Ariew, and Mark Perlman (eds.), *Functions: New Readings in the Philosophy of Psychology and Biology*. Oxford: Oxford University Press, 113–143.
Müller, Gerd B., and Stuart Newman, eds. (2003), *Origination of Organismal Form: Beyond the Gene in Developmental and Evolutionary Biology*. Cambridge, MA: MIT Press.
Müller, Gerd B., and Günter P. Wagner (1991), "Novelty in Evolution: Restructuring the Concept", *Annual Review of Ecology and Systematics* 22: 229–256.
——— (1996), "Homology, *Hox* Genes and Developmental Integration", *American Zoologist* 36: 4–13.
Neander, Karen (1983), *Abnormal Psychobiology*. PhD dissertation, LaTrobe University, Victoria, Australia.
——— (1991a), "Functions as Selected Effects: The Conceptual Analyst's Defense", *Philosophy of Science* 58: 168–184.
——— (1991b), "The Teleological Notion of 'Function'", *Australasian Journal of Philosophy* 69: 454–468.
——— (2002), "Types of Traits: Function, Structure and Homology in the Classification of Traits", in André Ariew, Robert Cummins, and Mark Perlman (eds.), *Functions: New Essays in the Philosophy of Biology and Psychology*. Oxford: Oxford University Press.
Owen, Richard (1843), *Lectures on the Comparative Anatomy and Physiology of the Vertebrate Animals, Delivered at the Royal College of Surgeons, in 1843*. London: Longman, Brown, Green and Longmans.
Pittendrigh, C. S. (1958), "Adaptation, Natural Selection and Behavior", in Anne Roe and George Gaylord Simpson (eds.), *Behavior and Evolution*. New Haven, CT: Yale University Press, 390–416.
Raff, Rudolph A., and Alan C. Love (2004), "Kowalevsky, Comparative Evolutionary Embryology, and the Intellectual Lineage of Evo-Devo", *Journal of Experimental Zoology* 302B: 19–34.
Roth, Louise V. (1999), "Within and Between Organisms: Replicators, Lineages and Homologues", in Brian K. Hall (ed.), *Homology: The Hierarchical Basis of Comparative Biology*. New York: Academic Press, 301–337.
Sattler, Rolf (1990), "Towards a More Dynamic Plant Morphology", *Acta Biotheoretica* 38: 303–315.
Schlosser, Gerhard, and Günter P. Wagner, eds. (2004), *Modularity in Development and Evolution*. Chicago: University of Chicago Press.
Shubin, Neil, Cliff Tabin, and Sean Carroll (1997), "Fossils, Genes and the Evolution of Animal Limbs", *Nature* 388: 639–648.
Wagner, Günter P. (1989), "The Biological Homology Concept", *Annual Review of Ecology and Systematics* 20: 51–69.
——— (1994), "Homology and the Mechanisms of Development", in Brian K. Hall (ed.), *Homology: The Hierarchical Basis of Comparative Biology*. New York: Academic Press, 273–299.
——— (2001), "Characters, Units and Natural Kinds: An Introduction", in Günter P. Wagner (ed.), *The Character Concept in Evolutionary Biology*. San Diego: Academic Press.

https://doi.org/10.1086/510172 Published online by Cambridge University Press

Weber, Marcel (2004), *Philosophy of Experimental Biology*. Cambridge: Cambridge University Press.
Wimsatt, William C. (1972), "Teleology and the Logical Structure of Function Statements", *Studies in History and Philosophy of Science* 3: 1–80.
Winther, Rasmus G. (2001), "Varieties of Modules: Kinds, Levels, Origins, and Behaviors", *Journal of Experimental Zoology* 291B: 116–129.
——— (forthcoming), "Parts and Theories in Compositional Biology", *Biology and Philosophy*.
Wouters, Arno (1995), "Viability Explanation", *Biology and Philosophy* 10: 435–457.
——— (2005a), "The Functional Perspective in Evolutionary Biology", in T. A. C. Reydon and L. Hemerik (eds.), *Current Themes in Theoretical Biology: A Dutch Perspective*. Dordrecht: Springer, 33–69.
——— (2005b), "The Functions Debate in Philosophy", *Acta Biotheoretica* 53: 123–151.

https://doi.org/10.1086/510172 Published online by Cambridge University Press