

Function, Homology and Character Individuation¹

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Many philosophers believe that 1) most uses of functional language in biology make implicit reference to natural selection and 2) the fundamental way in which biologists identify parts and processes in organisms is by their selected function(s). Both these claims are mistaken. Much functional language in biology refers to actual causal roles. The extensive biological literature on the 'character concept' focuses on another principle of biological identity, namely homology. This work is outlined and used to refute philosophical arguments for the importance and ubiquity of classification by adaptive function.

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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 'etiologically 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 etiologically theory embodies the standard neo-Darwinian view that biological teleology was rendered scientifically respectable by the theory of natural selection²:

"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 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 1993, Griffiths 1993):

- 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

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² The *locus classicus* is Pittendrigh (1958, 191-3). Important philosophical discussions include (Wimsatt 1972 see esp. 70; Brandon 1981).

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 (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 was once an adaptive trait, but not all adaptations are still adaptive traits and not every adaptive trait is yet an adaptation. If we use the language of functions, a trait is *adaptive* in virtue of some of its causal functions (those that contribute to fitness). A trait is an *adaptation* for functions which were causal functions contributing to fitness in ancestors, and so became selected functions.

In this paper I argue that much functional language in biology refers to causal function. Furthermore, enthusiasts for selected function are mistaken when they claim that selected function is the primary means by which biologists individuate the parts and processes of the organisms they study. Straightforward descriptions of the structure and causal function of parts and processes, and classifications of those parts and processes by homology, form the basis on which claims about selected function rest. *Pacé* selected function enthusiasts, those straightforward structural and causal functional descriptions do not contain implicit references to selected function.

My dispute with selected function enthusiasts thus concerns 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. ‘Character’ *simpliciter* refers to a determinable property (eye colour, a genetic locus) whilst ‘character state’ refers to a determinate value of that determinable (blue, AAATCG). 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 recognised 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). This discussion of the character concept proceeds against a general background assumption that characters are ‘homologies’ in one of the senses defined below: they are individuated by common ancestry or common developmental mechanisms³. In contrast, 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. Karen Neander is perhaps the leading advocate of this view. Neander’s (2002) defends her view against what she terms ‘functional minimalism’.

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

Functional minimalism is the view defended by Ronald Amundson and George Lauder and myself that disciplines like anatomy, physiology, molecular biology and developmental biology are primarily concerned with characters individuated by homology (Amundson and Lauder 1994; Griffiths 1994). Neander thinks that classification by selected function is more common in these sciences than either Amundson and Lauder or I allow. Neander is particularly critical of my (1994) account of homology. This account was certainly not adequate. The 1990s saw an explosion of new work as a result of the discovery of ‘deep homology’ in molecular developmental biology and the meteoric rise of the new discipline of evolutionary developmental biology (Hall 1992; Arthur 1997; Raff 1996) and I did not address these new developments until some years after the account Neander criticizes (Griffiths 1999). However, neither Neander’s criticisms of my (1994) account nor her own positive proposals are grounded in this recent literature on homology. Instead, her case for what we might call ‘functional revanchism’ (by analogy with the ‘revanchist’ desire of a nation to regain lost territory) is driven by the fundamental idea that has driven her work on biological categories for the last two decades (Neander 1983). Any classification of organisms into parts must allow there to be abnormal instances of each part. Neander argues that only a classification in terms of adaptive function will create categories that are ‘abnormality inclusive’. A similar theme has been important in Ruth Millikan’s work. Millikan (2002) argues that a biologically meaningful causal analysis of a system’s functioning (causal function) can only be conducted in the light of an understanding of the ‘proper functioning’ of the system (selected function).

What is ‘functional minimalism’? My view has always been that there are two fundamental aspects to the evolutionary process, common descent and adaptation. These give rise to two overlaid patterns in the distribution of biological characters, one captured by phylogeny and homology, the other by functional classifications. 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 their adaptive function (Griffiths 1994, 1996a, 1996b). Categories defined by selected function are thus important and ubiquitous. Neander, however, thinks that categories defined by selected function are still more ubiquitous: the characters which are grouped together by analogy are not, as I have argued, classified by homology, but are themselves classified by selective function. The main difference between functional minimalists and functional revanchists thus concerns function-talk 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. Functional minimalists maintain that unless these fields turn their attention to specifically evolutionary questions, they investigate function in the causal sense. Revanchists reply that they are always, at least implicitly, investigating function in the selected sense⁴.

⁴ This claim has also been ably criticized by Arno Wouters (2005a; 2005).

In contrast to the mass of philosophical work on selected function (Allen, Bekoff, and Lauder 1997; Buller 1999; Ariew, Cummins, and Perlman 2002), there has until recently been little philosophical work on homology (but see Matthen 1998, 2000). In my own earlier work homology is treated as a concept rooted in phylogenetic systematics. Recently, however, 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 (Love 2001, 2004; Love and Raff 2003; Raff and Love 2004; Brigandt 2002, 2003a; Winther 2001, In Press). 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 function, the importance of which has been evident at least since the rise of modern Darwinian approaches to behavior (Tinbergen 1951; Lorenz 1950).

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 an equivalence relation that groups characters into a hierarchy of equivalence classes; homologies can be identified at different levels of biological organisation; 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 forms a hierarchy of equivalence classes

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. When Neander writes that ‘Homology is a relation of degree, somewhat akin to the relation of resemblance or genetic relatedness’ (Neander 2002, 402) she must have been misled by an unusual usage of the word ‘homology’ in molecular biology (see below, 2.4) or by phrases like ‘closely homologous’. The latter refers to ‘taxonomic distance’, which is a measure on the topology of a cladogram or a phylogenetic tree, and no more implies that homology is a degree property than the claim that two species of birds are ‘closely related’ implies that membership of a taxon is a degree property. There are also cases have led biologists to talk of ‘partial homology’,

such as when the embryonic primordia that typically give rise to two different parts of a plant fuse to form a single part during the ontogeny of an atypical species (e.g. Sattler 1990). Some authors have also written of ‘partial homology’ when large characters in different species can be analysed into smaller characters only some of which are homologous. For example, some but not all regions of chromosome 2 in the D genome of hexaploid wheat are homologous to rice chromosome 4. Finally, some authors have spoken of ‘partial homology’ when two parts in different species share developmental mechanisms that are homologous (see next section). Neander does not mention these phenomena, but in any case they do not show that homology is a similarity relation, any more than the existence of hybrid taxa shows that taxon membership is a similarity relation.

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 (Capdevila and Belmonte 2001). More famously, 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 masculinisation of the fetus in *Ellobius* rodents and the male sexual characteristics that result from that process 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 whilst 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 whilst 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 infeasible, 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). Günther 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 4.2 below). 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 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 only works 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, 321-4; 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 realisable 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. Both ideas could be wrong, but the burden of proof is massively on the side of the sceptic. About two hundred years ago 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. The few sketches of scientific practice scattered through this paper give some idea of our current understanding.

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). A clade is a group of species which contains all and only the descendants of some ancestral 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 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 criticism seems to rest on her mistaken view that homology is a degree property. 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. Her emphasis). But the ‘character’ referred to in my definition is just this ‘specification of the traits in question’. The definition was intended to characterise homology as understood in cladistic systematics, and it should be read in line with the basic cladistic procedures described in my paper. In cladistic systematics homologies are inferred from a set of measured similarities between organisms, known as ‘shared characters’. Suppose we want to construct a cladogram using data concerning the DNA sequence coding for a suitable molecule in each species. Any pair of the aligned sequences 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 measurable property of an organism or only a property recognised as biologically meaningful in some theory of the organism. However, philosophers are familiar 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’ recognised in some philosopher’s ontology. My paper is 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 ‘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 cephalopod.

I suspect that Neander’s failure to recognise the possibility of using simple, operational characters as data to support a more theoretical claim about what the ‘real’ characters are reflects her view that no straightforward descriptions of structure or causal function in biology are possible without knowledge of the selected functions of the relevant characters. I discuss this view in Section 6.

4. Revanchism I: ‘Functional homologues’

Neander offers three arguments for functional revanchism. The third of these 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 sequences 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 does not use ‘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 mean by a ‘key innovation’. 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. Nonetheless, 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 homology is a degree property which does not allow any sharp boundaries to be drawn. Now, of course, homology is *not* a degree property, and even if it were, changes in selection pressure would not be a good place to look for sharp boundaries. 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. On this reading she is discussing the problem of ‘evolutionary novelty’ (Mayr 1960).

Insert Figure 1 about here.

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 ear ossicles, the incus, is homologous with the quadrate bone (fused to the skull) in reptiles and other tetrapods. This in turn is homologous to a region of the palatoquadrate bone in other teleosts, the clade that unites bony fishes and all terrestrial vertebrates. This character in teleosts is homologous with the dorsal portion of the mandibular arch (jaw) in sharks and rays, and this character in gnathostomes, the clade of jawed vertebrates, is homologous with the first gill-arch in jawless fish, such as the lamprey (Fig. 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 from gill arch to incus should be divided into three segments rather than two or four because there are two distinct changes of selected function, from breathing to ‘jaw support’ and later to ‘audition’. But, first, this is certainly not the only way in which biologists single out some 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.

These points are evident in Neander's own example. In standard presentations, the series is divided into five characters, not three, two of which, the palatoquadrate bone and the quadrate bone, function to support the jaw (the palatoquadrate cartilage is part of the jaw). The prominence of these five stages stems from the fact that they are the actual character states seen in major taxa – mammals, reptiles, bony fishes, cartilaginous fishes and jawless fishes. The fact that these five characters are not defined by their selected function in the way Neander suggests is evident from prominent theories about their evolution. The quadrate bone in reptiles, where it is fused to the skull, *does* play a role in hearing. It transmits vibration from the ground – something with obvious adaptive significance for both predator and prey. The transformation of the quadrate into the incus may have been driven by increased selection for hearing in early, nocturnal mammals. What creates an obvious break at this point in the series is not change of function, but the traditional morphological criteria – whether the bone is fused to the skull. Turning to the other character that Neander claims is defined by a selected function, an important recent study suggests that the initial evolution of the vertebrate jaw – the enlargement and more powerful articulation of the first gill arch to allow 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 biologists' 'key innovations' – features like the vertebrate jaw which allow 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, whilst 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 homologised to any preexisting character, such as the Chelonian (turtle) shell (Müller and Wagner 1991; for philosophical discussion, see Love 2001; Love 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.

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 fibres 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 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 seriously misunderstand Amundson and Lauder (1994). Neander argues that their account reduces to the view that biological classification is classification by structure alone (2002, 409-10). Even the title of their paper is misleading, she says, because it promises a defense of ‘the use of causal role functions in biology’ whilst 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 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 simple. She notes that the categories used in these sciences include abnormal instances.

A diseased heart is still a heart, and, to get away from that hackneyed example, 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’. 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. Although it is not essentially historical, the developmental approach to homology also yields abnormality inclusive categories: 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 vertebrae is serially homologous to my damaged third lumbar vertebrae for the same reason that it is serially homologous to my undamaged fourth lumbar vertebrae. 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 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. Birds and bats have wings for flying, so ‘wing’ is an analogy, but the avian wing and the chiropteran wing are homologies. Categories of analogy are essential when studying adaptation. To test a model of optimal wing design for maneuvering flight in a forest canopy, we need a representative sample of wings whose selected function is to enable their bearers to fly through dense forest. Part of being a ‘representative sample’ is taking into account phylogeny, as characters that are homologous to one another are not genuinely independent data points for this test. The use of these two classification schemes to illuminate one another is the ‘comparative method’ in biology (Griffiths 1996a) – we need both the ‘unity of type’ and the ‘effect of the conditions of existence’ to understand biological form (Darwin 1964, 206).

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 fn.12):

1. A character has a selected effect 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.

7. Selection and Biological Idealisation

I have shown that classifications by homology can be ‘abnormality inclusive’, but I suspect that many readers will be left wondering whether this is 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 – between those features designed by natural selection and those not so designed? In a recent paper Ruth Millikan has suggested that this 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 2002). Millikan’s concerns, and similar concerns voiced by Neander, point to an important issue, namely, the nature of scientific idealisation in the biological sciences. Darwinian populations are clusters of variation not constrained by any ideal type, but experimental biologists need to construct idealised 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 idealised 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 idealisation (see Griffiths In Preparation), I will briefly indicate some of the other 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 idealised cell is no different from an idealised model of a subduction zone in geology. The cell is not simplified in the biological 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. A model system is a practical idealisation – 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 idealisation 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.⁵ 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 standardised description of a biological system is simply 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 characterised 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 characterise an appropriate ideal system for analysis, there are many other contexts in which biologists use other forms of idealisation. This should not be surprising, since idealisation 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 idealised models of ecological processes.

8. Conclusions

1. 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).

⁵ 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).

2. 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.
3. Biological characters are primarily individuated by homology. Biologists use structural and (causal) functional descriptive characters, including relative position, embryonic origin, developmental mechanisms, gene expression, and so forth, to classify parts and processes by homology. The parts and processes classified in this way can, but need not, be assigned selective histories and selected functions in the light of their identity as homologues.
4. The claim that all biological description makes implicit claims about the selective history of the characters described is not supported by the 'argument from abnormality inclusive categories'. The body of established biological knowledge, which includes knowledge about selection histories, functions as background information in future investigations of any biological topic, including classification, but selection history does play the direct, foundational role in descriptive biology assigned to it by enthusiasts for selected function.
5. Enthusiasts for selective function have drawn attention to an important topic for future research – the nature of idealisation in the biological sciences – but their conclusion that idealisation is achieved by appealing to selection history is premature.

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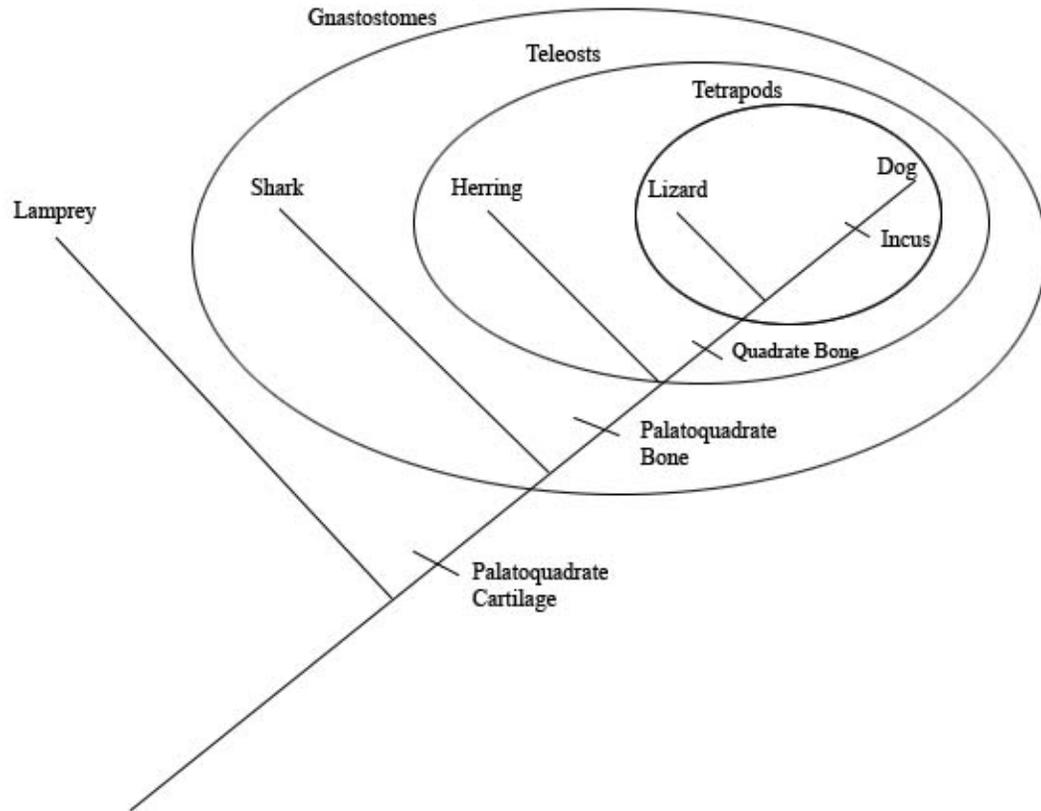


Figure Caption

Figure 1. Homologies of the mammalian incus.