Are Homologies (Selected Effect or Causal Role) Function Free?*

Alex Rosenberg and Karen Neander†‡

This article argues that at least very many judgments of homology rest on prior attributions of selected-effect (SE) function, and that many of the "parts" of biological systems that are rightly classified as homologous are constituted by (are so classified in virtue of) their consequence etiologies. We claim that SE functions are often used in the prior identification of the parts deemed to be homologous and are often used to differentiate more restricted homologous kinds within less restricted ones. In doing so, we discuss recent criticism of this view that has been offered (especially that offered by Paul Griffiths).

1. Introduction. Some philosophers have argued that all significant biological kinds—including homologies—are (implicitly or explicitly) to be characterized in terms of selected-effect (SE) functions, that is, ones with a "consequence etiology" (e.g., Neander 1991; Rosenberg 2006). Others have argued that many important biological kinds—including many homologies—are characterized in this way (Neander 2002).

By contrast, some philosophers and biologists have argued that homologies (as opposed to analogies) are *never* characterized by their SE functions. In particular, this claim has been made by those philosophers of biology who endorse the "causal role" (CR) account of functions due to Cummins, and by an overlapping group of philosophers of biology who argue that most important biological predicates are defined by homology, and in addition that homologous classification has no need of, or indeed no role for, SE functions. Among the most prominent of this

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†To contact the authors, please write to: Department of Philosophy, 201 West Duke Building, Box 90743, Durham, NC 27708; e-mail: alexrose@duke.edu or kneander@duke.edu.

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overlapping group are Amundson and Lauder (1994) and Paul Griffiths (1994, 2006).

Homology of biological traits or characters[1] is standardly defined as "sameness due to common descent," and we use this definition here (as did Amundson and Lauder [1994] and Griffiths [1994]).[2] But as philosophers will recognize, any definition that invokes vexed concepts such as "sameness" and "due to"—that is, caused by—is likely itself to be problematic. In this article we review the way homology claims figure in the classification of biological characters, and attempt to vindicate the importance of SE function in biological kinds. We argue (primarily in the first half of the article) that at least very many *judgments* of homology do after all presuppose, imply, rest on, prior attributions of SE function, and (primarily in the second half) that many of the "parts" of biological systems that are rightly classified as homologous are *constituted* by (i.e., are so classified in virtue of their) consequence etiologies.[3]

Some of our argument involves clarifying parts of Neander 2002 in light of subsequent developments, especially as found in Griffiths 2006. Two points are best mentioned immediately. According to Griffiths, Neander rejects Functional Minimalism, which Griffiths defines as the view that "disciplines like anatomy, physiology, molecular biology and developmental biology individuate character by homology" (Griffiths 2006, 3). However, Neander defines Functional Minimalism as "the view that there are no important functional categories in biology except perhaps for the analogous categories" (Neander 2002, 395) and it is instead this view that she rejects. This does not entail the position that Griffiths attributes to her. Neander says, for instance, "some homologous categories might be functional categories too" (398), so that "we can stress the importance of homology all we like and yet still say nothing to any effect against classification by function. . . . We can agree that homology is important without concluding that function is thereby unimportant" (399). And, "I agree that homology is important in the classification of traits. Where we differ is on the role of function" (392). Nor do we, in this article, deny the importance of homologous classification.

Griffiths further adds that, "Neander . . . thinks that *all* biological categories are at least partly defined by selected function" (2006, 13; emphasis in original). However, Neander says, "I will argue that homologous kinds are sometimes differentiated in terms of structure, sometimes in

1. We use "traits" and "characters" interchangeably.

2. This makes homology a historical concept. However, Griffiths (2006) distinguishes between "historical" and "developmental" homologies, as further remarked toward the end of the article.

3. On consequence-etiologies, see Wright 1976.

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terms of function, and sometimes, and often ideally, in terms of both" (2002, 392). She also allows for some classification by functions in the causal sense. Again, it is this pluralist claim on behalf of SE functions that we aim to establish here. In our view, biologists must very often reflect on SE functions in making judgments about homology and many very important biological kinds—including homologous kinds—are, constitutively, SE functional kinds. Ours is a pluralist position. In contrast, Griffiths, for instance, argues that "if functional classifications are to be of value to biology it must be because of their superior generality—the fact that they unite disjunctions of cladistic homologues" (1994, 213–214). In other words, he argues that SE functions have no role in biological classification outside of the analogous categories.

Neander's (2002) claim is that a notion of homology does not *suffice* for classification, even if we ignore the analogous kinds. She argues that many homologous kinds are also functional kinds ("functional homologues") because SE functions are often used in the prior identification of the parts deemed to be homologous and because SE functions are often used to differentiate more restricted homologous kinds within less restricted ones. This is also one message of the present article. Another important take home lesson from this dialectic between proponents of the indispensability of SE functions and the exponents of SE-free homologies is how theoretically intricate (not to say apparently circular, but in reality "spiral") even the most basic biological descriptions turn out to be. For if we are correct, homology—similarity due to shared ancestry or common descent—is a property of traits which are often individuated by their functions in the SE sense, and selected effect traits are traits with a certain type of ancestry, or that are in other words homologous.[4] Both homology and function, then, are notions shot through with Darwinian presuppositions about ancestry and adaptation. The difference between them is that homologies don't wear their adaptational pedigrees "on their sleeves," so to speak, while functions (SE functions) do.

Homologies are "sameness due to common descent" and we must ask what the sameness consists in, for it cannot consist purely in common descent. As Neander put it, "before two traits can be identified as homologous with respect to each other, we need some specification of the traits in question" (2002, 402). The traits adjudged the same cannot, on pain of circularity, be so judged on hypotheses of homology: their sameness or similarity can be explained by their common descent but it cannot merely consist in their common descent. If all there were to membership in a homologous kind were common descent, it would follow from Dar-

4. We assume rather than argue for the second part of the conjunction in this article, but it is not in dispute and is discussed in Neander 2002, 403–404.

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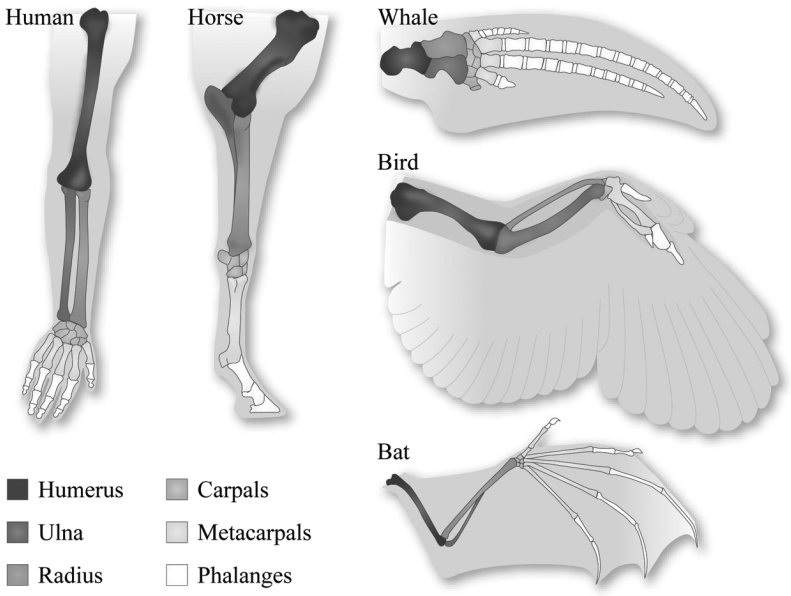


Figure 1. Variety of vertebrate forelimbs, all derived from a common ancestor and showing homologous bone structures. Note that the bat and the bird forelimbs are not homologous as wings.

win's hypothesis of common descent that every organ type is the same as every other, patently a reductio ad absurdum. If we are sensibly to define homology it must be treated as a diagnostic/explanatory kind that presupposes some prior categorization of traits. Therefore, the importance of homology notwithstanding, much remains to be said about how traits are classified.

Homology claims are hypotheses about common ancestors. SE function ascriptions are hypotheses about common ancestors as well, to which is added a hypothesis about selection. It is to be expected that, as we argue, the evidence for each such hypothesis is intimately related, and it should be unsurprising if, as we also argue, classifications based on homology often involve classifications based on SE function.

2. Homology Claims in Biology: The "Usual Suspects." One of the classic examples of a homologous structure is the vertebrate forelimb. One can see why biologists might conclude that the bones of the vertebrate forelimb (Figure 1) are homologous, that is, that their "similarity" is due to common descent. If one were to give the reasoning behind this conclusion it

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would consist at least in three points: the similar material composition of the bones of all these vertebrates, the similarity of complex topographic relations among the bones in each species' set of forelimb bones, and an account of how the differences in their shapes and structure can be expected from the adaptational problems which the forelimb addresses for each different species.

Homology claims are explanatory hypotheses. They presuppose causes for similarities. Accordingly, the similarities among traits for which such hypotheses are advanced are logically prior to homology hypotheses. As remarked in the introduction, the similarity can be explained by common descent but it cannot merely consist in common descent. Such circularity is avoided in the case of the vertebrate forelimb by the considerations adduced above: the similarity of the various forelimbs is pretty obvious, the material composition and structure of the hard parts of the forelimbs—the bones—are chemically very similar, and, more important, the topographic relations of the bones in each species are highly similar. In this case, such morphological criteria could perhaps suffice for prior specification of the similarities to be explained, and they are also highly suggestive of homology.

However, even in this case, adaptational considerations are important in an evidential sense. It is significant that the evident differences among the forelimbs are to be expected given the different environments (aquatic, avian, swamp, savannah, steppe, and forests) and the different tasks within those environments (swimming, walking, running, tool manipulation, and flight) to which they are adapted. Furthermore, these considerable differences in the tasks for which and the environments in which selection has shaped these forelimbs make a hypothesis of analogy or homoplasy to explain the similarities implausible to say the least.

Similarity in material composition and topographic relations might suffice for the identification of similarities to be explained in some cases, as just explained. However, such considerations are not always sufficient to ground a judgment of similarity that may be explained by hypotheses of homology. Consider two of the bones which in the mammal make up parts of the inner ear—the malleus and the incus (two tiny bones also known as the hammer and anvil, respectively).[5] These bones are homologous to two bones, the articular (homologous to the malleus) and the quadrate (homologous to the incus), which in some fish and reptiles constitute the jaw hinge. Both of these pairs of bones are homologous to

5. We expound this example, since it is employed by Griffiths as presumably favorable to his view. The example's prominence in the writing of the opponents of (SE) functional individuation may be due to Steven J. Gould's invocation of it. See the following footnote.

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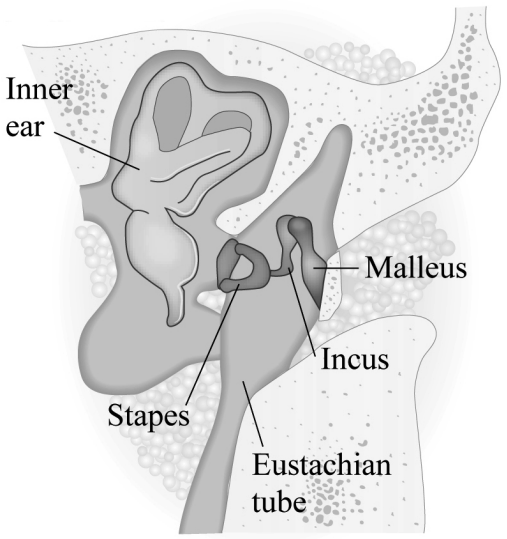


Figure 2. Mammalian inner ear.

structures that, in other fish, constitute gill arches. Figures 2–4 provide a comparison.[6] Figure 2 shows the malleus and incus of the mammalian inner ear. Figure 3 shows the articular and quadrate of a reptile jaw hinge and the malleus and incus of the mammal in relation to its jaw. Figure 4 is a schematic drawing of a gill arch. This is the boney structure to which the feathery gill rakes are attached. Fish have several such arches. Early fish had no jawbones and a series of these gill arches behind their mouths. In these early fish, which lacked bones, the gill arch was made of cartilage.

The homology of these sets of bones and cartilage have been celebrated among evolutionary biologists for a number of reasons, among them being the way in which paleontological evidence about them has both vindicated the fossil record's support for the theory of natural selection and undercut the confident claims of creationists that there are and could be no intermediate forms between these three sets of bones and cartilage.[7]

6. Our thanks to Matt Chansky for help with the diagrams. Figure 2 is adapted from Gilbert et al. 2006. Figure 3 is adapted from Vaughan et al. 2000.

7. See Gould 1993. In Gould (1994) 1997, 360–361, he writes: "The anatomical transition from reptiles to mammals is particularly well documented in the key anatomical change of jaw articulation to hearing bones. Only one bone, called the dentary, builds the mammalian jaw, while reptiles retain several small bones in the rear portion of the

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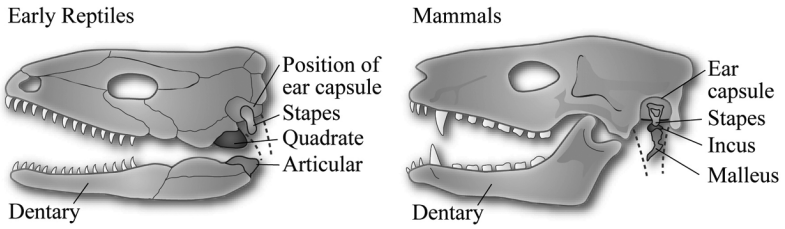


Figure 3. Side views of an early reptile's and mammal's jaw and ear.

3. How the Usual Suspects Illustrate the Role of SE Functional Judgment in Homology Claims. As Griffiths (2007, 2009) notes, three principle criteria for judgments that distinct parts are homologous as opposed to merely analogous are (*a*) identity or similarity in the relative position of parts in the two organisms, to which may be added identity or similarity in composition and topology if not topography;[8] (*b*) the parts sharing some trait which can play no SE or CR function in the economy of the organism (this criterion was especially emphasized by Darwin); and (*c*), where conditions *a* and *b* are not satisfied, the two parts can be subsumed under a single homological kind via a chain of intermediary parts that do satisfy criteria *a* and *b*.

These sets of body parts, the inner ear bones of mammals, the jawbone connectors of some jawed fish and reptiles, and the gill-arch cartilage of jawless fish do not obviously satisfy criteria *a* and *b*. While there are

jaw. We can trace, through a lovely sequence of intermediates, the reduction of these small reptilian bones, and their eventual disappearance or exclusion from the jaw, including the remarkable passage of the reptilian articulation bones into the mammalian middle ear (where they became our malleus and incus, or hammer and anvil). We have even found the transitional form that creationists often proclaim inconceivable in theory—for how can jawbones become ear bones if intermediaries must live with an unhinged jaw before the new joint forms? The transitional species maintains a double jaw joint, with both the old articulation of reptiles (quadrate to articular bones) and the new connection of mammals (squamosal to dentary) already in place! Thus, one joint could be lost, with passage of its bones into the ear, while the other articulation continued to guarantee a properly hinged jaw. Still, our creationist incubi, who would never let facts spoil a favorite argument, refuse to yield, and continue to assert the absence of *all* transitional forms by ignoring those that have been found, and continuing to taunt us with admittedly frequent examples of absence."

8. A topographic similarity is one of (rough) geometrical congruence. A topological similarity is one that could result from any deformation that does not divide the part into spatially separated regions. Plainly, topological similarity is rarely a sufficient basis for the sort of similarities that homology explains. Indeed, homologies may obtain between bones that are topologically continuous and ones that are not.

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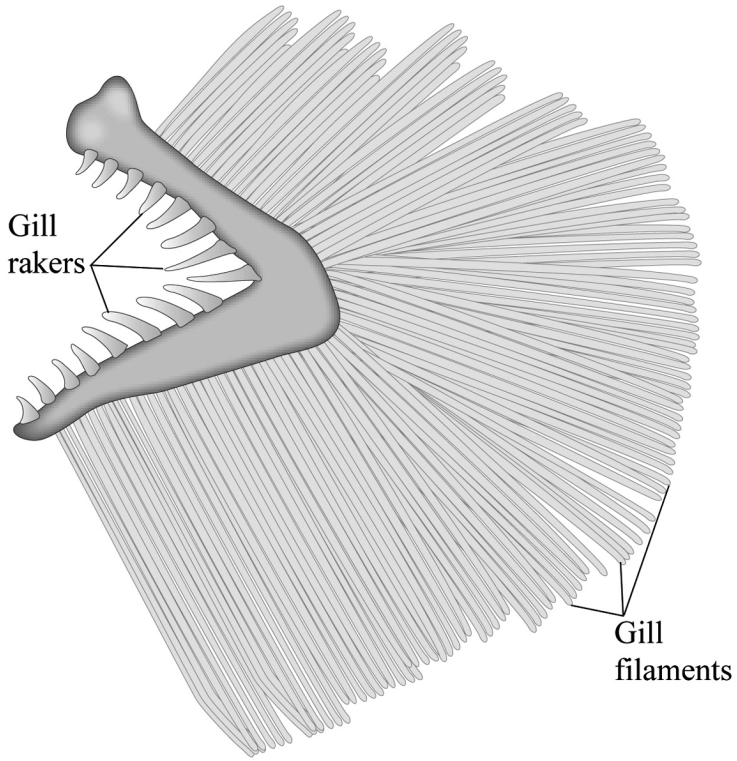


Figure 4. Gill structure.

significant similarities, there are also significant differences, one reason why this has been such a celebrated case. For instance, mammals have three inner ear bones, reptiles have only one; reptiles have two other distinct jawbones besides the articular and the quadrate, while mammals have just the one. The jaw hinge of reptiles is formed by the intersection of the quadrate and articular, whereas the mammalian jaw hinge is formed of different bones (the dentary and squamosal), and the malleus and incus are in the ear. Nor are they compositionally the same, or even similar enough (in their adult forms) to provide a sufficiently firm basis for any judgment that they are the same type of body part, or similar to one another in respects that require special explanation. Though all connective tissue in vertebrates shares some similarities, these similarities are not peculiar to the sets of body parts under discussion. Moreover, there are many differences between bone and cartilage with respect to the abun-

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dance and types of cells, the proportion of cells to extracellular matrix, the ground substance of the matrix (whether it is mineralized), and so on.

Nor, if we ignore developmental considerations (to which we return in a moment), do the homologous pairs share any special nonfunctional morphological trait that clearly cries out for explanation in terms of common descent. In fact, there is considerable structural, and topological evidence against similarity on criteria *a* and *b* among these traits. Why should physically diverse structures which came to function in hearing and in biting be similar with ones that function to filter for food and oxygen so that such an explanation of their similarity is motivated? Of course, current dissimilarity of function is no basis for some sort of explanation-demanding similarity.

It is primarily criterion *c* the existence of a chain of intermediaries that the biologist relies on to ground judgments of similarity to be explained as homologies. As paleontologists note, in their glee to refute creationists, a number of forms intermediate between the gill supports and the reptilian jawbone and mammalian inner ear have been discovered. These intermediaries provide greater similarity between the pairs in more closely related species. But considerations used to establish this chain of intermediaries—that is, that they are intermediaries—often concern SE functions. Two kinds of considerations have been particularly important in this case. One kind of consideration involves overlapping SE functions. In some of these intermediaries, the bones have more than one function. For example, in *Morganucodon* (small mammals of the Upper Triassic), the quadrate and articular serve as ear bones *and* jawbones simultaneously (Kermack, Mussett, and Rigney 1981). Modern reptilian quadrate and articular jawbones also serve in a rudimentary way to transmit sound to the stapes and the inner ear. Comparative anatomists describe the transition from jawbones to inner ear bones as one in which bones initially located in the lower jaw are selected for hearing by variations that detach them from the lower jaw and move them to the ear (Kardong et al. 2002). A second kind of consideration involves functional "redundancy." It is because there are a series of gill supports in jawless fish that the first in the series can evolve into the jawbones of jawed fish. And it is because the jaws of the common ancestors of reptiles and mammals consisted of four bones that it was possible for some of these bones to migrate to the ear, without the necessity of passing through a period of evolution during which the jaw was nonfunctional (as the creationists had maintained). Thus apparently dissimilar traits can be identified as "the same" through a chain of transformations that selection can explain, and this explanation supports the hypothesis of homology.

A considerable part of the argument for homology here is SE functional. It is because the different structures can be understood in terms of a

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process of adaptation, at times for overlapping roles, that the biologist concludes that there is a basis for similarity or "sameness" despite large differences in both form and function.

There is another important basis for the similarity judgments about the incus/malleus pair and the quadrate/articular pair and the gill arches. In embryological development, *corresponding* structures in fetuses give rise to these pairs. So, they (along with other characters) share a developmental source. But this shared source, this new similarity, raises another question: on what basis does the fetal structure that is the source of the pair of bones in mammals constitute the *same* trait-kind as the embryo structure that is the source of the reptilian pair, or for that matter the same kind of structure as the developmental source of the pair of jaw connectors of boney fish and the pair of gill arches of cartilaginous fish? The similarities between the developmental stages of the homologues are certainly suggestive, but had they been compelling on their own, comparative embryology would have been a lot easier, von Baer's "laws" less a subject of controversy,[9] and the tree of life far more obvious a fact than it seems at first blush to be. In any event, the importance of embryological evidence concerning homology does not change the fact that reasoning about SE functions is also important.

Nowadays these claims concerning sameness of developmental parts are, in part, being cashed in for sufficient similarity in the types, numbers and order of homeobox genes. Nonetheless, this does not negate the points made above either. Judgment of homology still depend on understanding many differences in terms of transformations in *selected effects*. Roughly, in the case under discussion, the judgment is that the earliest structure persists over time because it was selected for giving rise to gill arch cartilage, variation in this ("same structure") was subsequently selected for giving rise to jawbone hinges, and that ("same structure") was in turn selected for giving rise to inner ear bones in mammals. Evidence for sameness in the line of descent is partaking in overlapping parts of a series of consequence etiologies.

Of course, owing to Darwinian gradualism, in the long run and if paleontologists are fortunate, a range of intermediate forms could be found which makes gradualist "sense" out of structures radically different in shape, location and topographic locations (differences great enough to be paraded by creationists). Such a program of research eventuates in the

9. There are three "laws": (1) The general characters of the larger group to which an embryo belongs appear earlier in development than the more specific characters of the smaller group; (2) the more specific the character, the later it appears in development; and (3) the embryo does not pass through the forms of ancestral creatures, but rather progressively separates itself from them.

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exhibition of developmental and adult gradients of form, such as those elaborated by D'Arcy Thompson ([1917] 1992). But it proceeds on a prior commitment to overlap of *functions* among developmental structures that give rise to the diverse instances arranged in a gradient of changes in form.

When can a judgment of biological similarity avoid making recourse to selected effects altogether? There is no general recipe, but a consideration of nucleotide and amino acid sequence structure shows how limited such cases might be. When a character can be unambiguously described in nonbiological terms, similarities—indeed identities—can be established free from functional hypotheses. In the simplest case, short sequences of either nucleotides or amino acids may be molecule-for-molecule structurally identical (often without having any function—e.g., "noncoding multiple repeats"). However, considerations of SE function still play an evidential role in establishing homology. The longer the linear sequence of a pair of DNA strands or a pair of polypeptides (proteins) are molecule-for-molecule identical, the greater is the likelihood that their similarity is biologically significant, and calls for explanation (usually as homologies, much more rarely as analogies). Even when the match is not perfect, though, there may be similarity among such pairs of molecules that is ground for seeking an explanation in terms of homology. When two somewhat different DNA sequences produce the same protein or similar ones with the same enzymatic role, there is also good reason to conclude that they are homologous, especially when most of the differences in gene sequence do not make a difference to the structure of the protein they code for. The regions of the two genes that are the same in sequence are said to be "conserved" by selection, and the differences are credited to neutral point-mutations. These judgments of homology are thus made in the context of background judgments about the SE function of the sequence as a whole, and such gene sequences are often characterized in terms of their SE functions. Functional individuation will closely approximate sequence identity when we exclude from consideration "neutral" substitutions that do not change amino acid codings, or codon differences that only change amino acid sequences far from the enzymatically active or allosteric sites, and are therefore also selectively neutral.

In any event, almost immediately "above" the level of primary nucleic acid and amino acid sequence, the multiple realizability of biological traits grows so rapidly that compositional and topographic differences will often make SE functions (of developmental and intermediate structures) indispensable for character individuation, as in the case of the inner ear bones, the jawbones and the gill arches of mammals and fishes.

One general conclusion to which these considerations drive us is epistemic: in order to make a well-grounded judgment of homology—that

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is, to *explain* a biologically significant similarity, the biologist must advance a prior hypothesis of "sameness" or "similarity," that will often be as complex a theoretical judgment as any claim about SE functions, indeed it will often be a claim about such functions.

There is also a more "metaphysical," or at any rate constitutive, claim to be made, one that is independent of the epistemic point but reinforces it. This is about the nature of biological kinds and it is driven by the adaptational program of Darwinian biology. Recall Gould and Lewontin's (1979) famous attack on the adaptationalist's penchant for "atomizing" the parts of the organism and attributing separate SE functions to each of them. It is now recognized that common sense biological taxonomies and observationally driven individuations do not map smoothly onto the real kinds of biology and the adaptational scenarios that brought them about. The role of constraints, Bauplane, drift and preadaptation now qualify the adaptationalist program. Nevertheless, biologists hold that these four sources play a supporting role to selection in the emergence of biological parts, traits and characters from physical and chemical processes. To the degree that this is so, the kinds of biology—not just the species, but types of body parts, tissues, organs, cells, organelles, and so on—must have been shaped by consequence etiologies, that is the combination of their advantageous effects and their common descent working together. On a more methodological note, only a thoroughly instrumental science, or a thoroughly observational one, can avoid reflecting the causal forces that shape its domain in its classification of that domain.

Any particular adaptational taxonomy is of course a hypothesis about the past—immediate and distant. And testing it will certainly require the employment of descriptive vocabulary that does not imply the truth of the *particular* adaptational hypothesis under test. This methodological demand may be mistaken for a much stronger, unreasonable requirement that a given adaptation hypotheses be tested by data described independently of *any* adaptational hypotheses. The functional anatomists' determination of the shape and composition of a particular bone, and its relationship to other bones—its form and (CR) function, can certainly be free of any prior assumption about the specific adaptational scenario that brought about its form and function. But even that it is a bone, as opposed to a mere chunk of calcium carbonate, presupposes an adaptational hypothesis. More concretely, when paleontologists conclude that an ancient skull is that of a hominin by quantitative comparison of its shape and size, especially the bumps in it, to that of a known hominin, they have already helped themselves to several adaptational hypotheses behind the description of the items compared, as bones, skull part, brain case, oxcipital lobe, and so on. (Thus the spiral nature of these concepts, mentioned earlier.)

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Amundson and Lauder have famously written,

> In the functional anatomist's vocabulary, [physical] form and [CR] function were both observable, experimentally measurable attributes of anatomical items (e.g., bones, muscles, ligaments). Neither form nor function was inferred via evolutionary history. (1994, 449)

True enough as far as it goes. The particulars of form are observationally determinable, at least in the case of individuals of extant species. But that they are biological parts, and which parts they are, and what is homologous with what, is not a matter merely of observation and measurement. A slightly more searching analysis of the vocabulary of the functional anatomist will reveal that it is shot through with terms intelligible only as names of parts with SE functions.

4. Griffiths, Amundsen, and Lauder on Homology. Griffiths argues that, "if functional classifications are to be of value to biology it must be because of their superior generality—the fact that they unite disjunctions of cladistic homologues" (1994, 213–214). Thus he argues that if functional classifications are to be of value to biology they must be analogous, rather than homologous, classifications. Later, in "Function, Homology, and Character Individuation," he writes,

> I defend the view that many biological categories are defined by homology against a set of arguments designed to show that all biological categories are defined, at least in part, by selection function. . . . I show that classification by selection function are logically dependent on classifications by homology, but not vice versa. (Griffiths 2006, 1)

And later, "characters are homologies: . . . they are individuated by common ancestry or common developmental mechanisms," and "homology is a relation of biological sameness" (5). Amundsen and Lauder concur, maintaining that

> whatever the favored definition of homology, one feature of the concept is crucial: the relation of homology does not derive from the common function of homologous organs. Organs that are similar in form not by virtue of phylogeny but because of common biological role (or SE function) are said to be *analogous* rather than homologous—they have similar SE function and so evolved to have similar gross structure. . . . The fact that anatomical or morphological terms typically designate homologies *shows that they are not functional categories.* (1994, 455; emphasis added)

How to interpret the latter (italicized) claim is open to dispute, but we

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take them to mean, minimally, that SE functional kinds are not logically prior to homologous kinds and that the latter do not logically depend on the former.

Griffiths makes two claims. SE functions are logically dependent on homology, but homology is not logically dependent on SE function. There is no dispute over the first of his claims: SE functions arise when *lineages* of traits are selected for certain of their dispositions and the notion of an SE function is moreover defined in terms of what a lineage of traits was selected for.[10] Since the first of his claims is not in dispute, we therefore focus on the second, which Amundson and Lauder also make.

We maintain that Griffiths' and Amundson and Lauder's understanding of homology is at variance with the biology reported in Section 2 and Section 3. As introduced above, homologies are invoked, and contrasted with analogies, to explain and group together characters that have already been individuated, an individuation that often involves thinking about selection history and selected functions.

To articulate his own and Amundsen and Lauder's account of the nature of biological concepts, Griffiths erects a view which he calls "functional revanchism," which he attributes to Neander.

> **Functional Revanchism**. The biological sciences are always at least implicitly investigating function in the selected-function sense.

By contrast, he attributes to Amundson and Lauder and also endorses the view 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" (Griffiths 2006, 3). This attributes to Neander (2002) a stronger and more sweeping claim than she makes, and weakens the claim she was opposing, since the biological sciences are turning their attention to specifically evolutionary questions whether it is homology or analogy that they are considering.

Of course, we do not want to deny that biologists investigate "functions," in the causal sense, if all that this means is that, among other things, they investigate what traits do, and do that is adaptive, and so on. However, as long as we are not taken to be denying this, we agree that "functional revanchism" captures one end of a spectrum towards which we probably approach more closely than they do. We believe that the biological sciences are very often, at least implicitly, investigating function in the selected-function sense, even when they turn their attention

10. Neander (2002, 404) points out that, for this reason, not even in her earlier work (1991) remarks to the effect that traits are always classified by (SE) function ought to have been interpreted as a denial of the importance of homology.

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away from specifically evolutionary questions. However, we are not here to discuss so very large a topic.

Our interest is in the more specific question of how homology is determined and how homologous traits are classified. If "functional revanchism," is to name a position that the authors of this article share and that is at issue, it names the claims that (i) one must often reflect on SE functions in determining homology, and (ii) many very important homologous kinds of traits are in part constituted by SE functions. The first part of this article has established the first claim. We turn now to the second. Griffiths' view is that *no* important homologous kinds are in part constituted by SE function. He sees a "stark contrast" between "the view that biological categories of parts and processes are defined by their selected function" and the assumption that "characters are homologies" (Griffiths 2006, 4). We see no such stark contrast. We claim that the two are complementary.

Against Neander's 'functional revanchism', Griffiths (2006) seeks to establish 3 theses about homology as a (SE) function-free basis of biological classification.

1. Homology defines a hierarchy of sets of characters—like taxa, homologous parts of organisms form groups within groups.
2. There are levels of homology: evolution can preserve a morphological structure while transforming the molecular mechanism that produces it and conversely can redeploy an existing molecular mechanism to underpin development of a novelty.
3. There are two distinct homology-concepts: (*a*) taxic or Darwinian homology (which in Griffiths 1994 were called "cladistic homologies") and (*b*) developmental homology.

We find his use of 1 puzzling, for this is a point that Neander (2002) was at pains to stress. Homologous groupings of traits do, to be sure, form hierarchies. Larger, more inclusive groups of homologous characters can be divided into more fine-grained, more closely related groups, in a hierarchical fashion. Neander argued that we thus "have ways of distinguishing smaller homologous groupings within larger homologous groupings" (2006, 402),[11] and therefore that the fact that classifications of char-

11. Griffiths interprets Neander's comment that "homology is a relation of degree, somewhat akin to the relation of resemblance or genetic relatedness" (Neander, 2002, 402) as appealing to Darwinian Gradualism. But her point was that traits can be *more or less closely* homologous, and that just as we must specify the respects in which two items resemble each other we must also specify the respects in which two items are homologous. Her argument does not rely on Gradualism. Nor should she be read as claiming, as Griffiths (2006, 12) suggests, that homology relations behave formally like a measure of *overall* similarity, which is quite contrary to her view.

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acters are homologous leaves open the question of what further classificatory principles are involved. The earlier arguments that Griffiths (1994) and Amundson and Lauder (1994) had offered against (SE) functional categories had been arguments for the importance of homology, seeming to imply that this by itself could show that (SE) functions were unimportant. However, this is not so. Vertebrate forelimbs are a homologous classification, but certain less inclusive homologous kinds—of fins, legs, arms, wings, flippers, and so on—are differentiated by their SE function.[12] Robin wings are homologous to human arms in *some* respect or respects (e.g., *as vertebrate forelimbs*). But robin wings are also homologous to the wings of a blackbird in some *other* respect or respects (e.g., *as wings* or, in other words, as limbs *adapted for flight*). Once we have acknowledged the importance of homology, we are still left with the task of explaining the further principles of classification.

Note that the hierarchy of homologies means that if SE functions are required to establish similarity at lower levels of the hierarchy, as we argued was the case in Section 3. Their roles in determining similarity will continue to be carried by higher-level homologies even when they are not easily visible at these higher level.

Perhaps another claim can also be made. If homology is similarity *due to* descent then homology is an explanatory concept, for homologies will explain the correctness of cladistic taxonomies in the way that atomic theory explains the correctness of the Periodic Table of the Elements. Griffiths wants to treat homologies in the way Mendeleev ([1869–1905] 2005) treated chemical reactivities, as diagnostic, not explanatory grounds for classification in his period table of the elements. There is of course no noncontroversial analytic/synthetic, or classificatory/explanatory distinction, but there is a difference and Griffiths does not accept that homology lies on the explanatory side of biology. He treats 'homology' as the basement level classificatory scheme in biology.[13]

We also agree that 2 is a correct observation but again disagree that it tells against our position. On the contrary, it reflects the degree to which homology attributions are explanatory and rely on a great deal of biological theory. Thesis 2 makes it plain that judgments of developmental homology cannot always rely on uncontroversial purely structural characterizations of nucleotide or protein product molecular sequence. Rather, they presuppose theoretical judgments of similarity that are likely to be based on or qualified by SE functional analyses of gene action. How, after all, can an underlying molecular developmental pathway be judged to

12. Of course, not all vertebrate wings are homologous as wings.

13. But cf. Griffiths 2007, in which he recognizes the explanatory role of homology.

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remain the *same* pathway to the *same* morphological structure, during a substantial or even largely complete turnover of its nucleotide sequence foundation? Shades of the ship of Theseus!

Amundson and Lauder (1994) allege that the (SE) function-free homologous kinds they advocate are "more observational" and "less inferential" than those that rely on (SE) function, thus intimating that the former are to be preferred. But as Neander (2002) argued, and as we argue here, claims of homology are highly inferential, and 2 gives us further reason to reject their allegation.[14]

This also has implications for 3's distinction between what Griffiths calls taxic or Darwinian homology claims and developmental homologies. As in the case described in Section 3, when similarities among adult forms are unobvious, taxic homology judgments will require developmental homology grounds. Indeed, there is good reason to hold that developmental homology judgments will completely undermine taxic homology claims when they conflict. If two topographically, structurally or topologically similar traits can be shown to emerge developmentally from distinct pathways that begin at diverse genetic loci (not themselves homologous through duplication events for example), it is hard to see what reason there is for treating them as homologies instead of analogies.[15] Griffiths concludes:

> 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. 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. (2006, 11)

These are not obvious and anodyne observations. We dissent from them, owing to a fundamentally different appreciation of the role of biological

14. Their claim that significant biological classifications were observational rather than inferential lead Neander (2002, 409–410) to wonder if they saw no constitutive classificatory role even for homology, because the claim seems to presuppose nonhistorical criteria. Historical criteria would seem to be inevitably "inferential." Thus Neander argued that the classifications were 'essentially historical'.

15. Arguably, this evidential primacy of developmental homology reflects the special role of the genome, including RNA and DNA, in carrying information about traits (a claim which Griffiths has elsewhere rejected, in, e.g., Griffiths and Grey 1994).

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theory in classification. To begin with, it is not a manifest fact but an inferred conclusion that the *same* part (and process) kinds or types can be found in different organisms. For, as we have seen, *sameness of part* is a theoretically tendentious conclusion, one that requires considerable theoretical apparatus. Homology and its sister concept, analogy, do not describe phenomena to be explained; they provide different explanations for similarities which biologists' operational measures have uncovered since the nineteenth century.[16]

5. What Is Wrong with Functionalist Revanchism? Griffiths addresses several arguments that he attributes to Neander 2002. "Functional revanchism" begins with the observation made frequently so far in this article, as Neander (2002, 402) expresses it, and Griffiths quotes it: "before two traits can be identified as homologous with respect to each other, we need some *specification of the traits* in question" (2006, 12). Neander (2002, 401–402) argued that cladistic divisions alone cannot serve to classify traits, because clades do not allow us to draw the required biologically significant distinctions among traits that are within clades.[17] Consider the clade that starts when gill arches appear and goes on to include fish and reptiles with jawbones and mammals with inner ear bones. SE functional characterizations, in contrast, distinguish inner ear bones from jawbones and these in turn from gill arches. They thus provide the resources that experimental or evolutionary biology requires to make obvious distinctions between traits of mammals, reptiles, boney fish, and cartilaginous ones. Whence the capacity of SE functions to carve nature's joints more finely.

Griffiths' response is interesting and revealing for it turns on a counterexample from molecular biology, where similarities and differences are easier to establish chemically, without appeal to function, just as noted in Section 3.

> In cladistics, homologies are inferred from a set of measured similarities between organisms, known as shared characteristics [not 'characters'—a term Griffiths reserves for homologous traits]. Sup-

16. Richard Owen introduced the term "homology" in 1843, but it does not follow that he had a merely developmental concept in mind. In his view, homologous characters were from the same "plan," an embodiment of the same "idea."

17. Griffiths claimed that, "A homologous trait is a character that unites a clade" (1994, 212). Griffiths says: "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 (in 1994) to as 'cladistic homology'. My [1994] definition is inadequate because it takes no account of the approaches to homology described above (developmental and serial homology)" (2006, Section 3).

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> pose 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 points and different at others. When they are identical, this shared character [*sic*] may be a homology or it may be a homoplasy. . . . When we say that the character state of the first nucleotide in each sequence is C[ytosine] we are giving a *physical* specification. (2006, 12)

Thus, Griffiths concludes, we can specify the "shared characteristics," which judgments of homology require, without invoking SE functions. However, Neander (2002) does not maintain that there are no homologous classifications that are defined in terms of structure, but agrees that some are. Her claim is that there must be *some* specification of the trait, and that this is sometimes in terms of SE function. Her position was (and our position is) a pluralist one.

In any case, Griffiths needs, at a minimum, a counterexample from a level of organization where there is no scope for recourse to physics and chemistry to establish uncontroversial identity or similarity. If homologies were called upon to explain only similarities in molecular sequence, we could more easily dispense with (SE) functions. But Griffiths is perhaps the last philosopher to make this concession. He not only rejects the claim that genes can be individuated by their molecular sequences,[18] and rejects the centrality of the gene in determining biological traits—characters—but, as his elaboration of Thesis 2 above notes, cladistic or taxic homology will sometimes remain the same under changes in underlying molecular mechanisms. Further, since Griffiths makes the remarkably strong claim that SE function is *never* involved in trait classification, outside of the analogous categories, it is incumbent on him to show that this stability of homologous kinds never rests on the stability in (SE) functions. To repeat, our position is a pluralist position; it is not incumbent on us to show that it always is.

So, how do we draw distinctions between biologically important characters, such as inner ears, jaw hinges, and gill-rake supporters within individual clades? Neander's suggestion is that "one main way in which this is done is by drawing conceptual lines at those places where there is significant change in what there was selection for" (2002, 403). She also points out that there is selection for dispositions (the SE, as it were) and selection of the structures and mechanisms that are responsible for them, and argues that these are but two sides of the same coin and can each have complementary classificatory roles. Selection for supporting gill rakes creates the gill arch, selection for biting changes the gill arch into the jaw

18. See, e.g., Griffiths 2009.

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hinge, and selection for hearing moves bones that used to hinge the jaw away from the jaw so they can play a role in hearing. In our view, the different stages of this selection history provide a particularly fruitful basis for differentiating among the traits involved.

What is wrong with this claim, according to Grifiths? First, that the three pairs of bone and cartilage are not defined in terms of their selected function "is evident from the usual theories about their evolution" (2006). It is unclear what he has in mind by this, but keep in mind that "functional revanchism," if it be something we support, is not the view that (SE) functions are the sole basis of classification, only that they are an important one. He continues with what might be a second or a supporting point: in some reptiles one pair of bones sometimes discharges both functions of jaw hinge and hearing. But this does not tell against our view. Classifications can involve more than one SE function. Moreover, the consideration adduced by Griffiths is one of the most powerful arguments for the claim that reasoning to homologies rests on attributions of SE function. After all, the topographic and compositional differences between inner ear bones, jaw hinges and gill-arch cartilage are so great as to have made SE functional considerations indispensable to judgments that they also constitute instances of a single, more inclusive kind, and require a homology explanation.

Griffiths' third argument might almost seem to be a strong consideration in favor of "functional revanchism," in the light of our discussion in Section 3.

> 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 bone in all other osteichtyans (boney fish) *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 the comparative anatomists looking for a way to bring their descriptions of different vertebrate skeletons under a single, general account of the structure of the vertebrate skeleton. (Griffiths 2006, 15; emphasis added)

As Griffiths indicates, the quadrate bone of fish has little resemblance to the contemporary mammalian incus, other than that both are derived from a single type of structure. In making their apparently counterintuitive claim that the incus is a modified quadrate so as to make Darwinian sense out of the very different vertebrate skeletons (it was not anything like as easy as the vertebrate forelimb), the comparative anatomists relied on the fact that differentiation of function could drive a single structure into two different ones. Thus the judgment as to their sameness of kind depends

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on understanding the differentiation in their SE function. However, Griffiths' point here seems to be that we can classify the mammalian incus and the quadrate of fish into *distinct* kinds on the basis of morphological criteria alone. He suggests that there is, in this respect, "an obvious break . . . in the series" (2009) and hence that the different SE functions are not needed for their classification into two distinct kinds. Our "functional revanchism" has a place for morphological criteria, as noted above, but Griffiths' argument is anyway overly hasty. That one can easily tell apart instances that are distant from transitional forms does not show that there is an "obvious break" in the series. Nor does an ability to tell them apart by virtue of their morphology demonstrate that functional criteria are not involved. (Consider that we can easily tell a cup from a saucer on the basis of their shapes, and yet it does not at all follow that functional considerations are irrelevant to the one being a cup and the other a saucer.)

Another argument for "functional revanchism" that Griffiths attributes to Neander and seeks to rebut relates to her allusion to the manifestly evident fact that many experimental biologists, for example physiologists studying muscle fibers, persistently employ functional vocabulary and their research programs are guided by functional attributions. "The problem with this appeal to practice is that it equivocates on two sense of the word 'function': actual causal roles (Cummins functions) and selected effects," says Griffiths (2006, 16–17). The former, he insists plays an important role in classification. Griffiths continues, "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." And a moment later, "not marking this distinction causes her to misunderstand Amundson and Lauder" (17).

However, neither Amundson and Lauder (1994) nor Griffiths (1994) had seemed (at least to Neander) to concede any *classificatory* role to functions of either kind outside of the *analogous* categories. Though Amundson and Lauder (1994) speak of *biological investigation* into causal-role functions, one can search their paper in vain for any description of their role in *classification*. And Griffiths writes (as quoted before) that, "if functional classifications are to be of value to biology it must be because of their superior generality—the fact that they unite disjunctions of cladistic homologues" (i.e., it must be because they form analogous kinds) (1994, 213–214). Griffiths (2006) has since clarified that he intended here only to refer to SE functions, and it is worth emphasizing the importance of this clarification given the recent tendency amongst a variety of authors toward the view that functions (unqualified) are not required for trait classification. But, in any case, Neander (2002, 393) marks the distinction between SE functions and CR functions and explicitly prefaced her whole paper on what she took to be a shared assumption: that *if* functions were

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implicated in *abnormality inclusive* categories (categories that include malfunctioning instances) then they were SE functions. Though this assumption is now revealed as *not at all* shared, there remain two points that can be made: (*a*) that functions of some kind are involved and (*b*) that specifically SE functions are. The discussion of muscle fibers addressed *a*.[19] We fine-tune the argument for *b* as distinct from *a* in the light of recent clarifications below.

Before we do this, it is worth noting that if we reach back for a moment to even earlier discussions of this issue, the dialectical ground shifts again. At one point, proponents of the classificatory importance of SE functions were defending their view against the idea that Cummins-style causal-role functions could suffice as an *a*historical alternative, and one that many (particularly in philosophy of mind, but also in philosophy of biology) thought preferable on those grounds.

At least Griffiths (2006) and, according to him, also Amundson and Lauder (1994) agree with "functional revanchists" on this: that functional considerations of some kind are important in the classification of traits, and not only in the case of the analogous ones, and that at least some homologous classifications are historical. So much of what we have been defending all along is therefore either restored or was never really withheld by these authors: that is, many trait classifications are both functional and historical.

The remaining issue would then seem to be whether SE functions are needed, or if only causal-role functions combined with homology are. The gap between opposing views will have shrunk, and will now need to be more delicately defined than before.

Now, an SE function depends on there being a *lineage* of traits which has undergone selection for a Cummins' style causal-role function, give or take a few niceties (e.g., Cummins' causal-role functions are essentially interest-relative, a feature that we do not endorse, but which we can ignore here given that it has played no role in the arguments offered on either side). It is clear that Griffiths agrees that 'causal functions' are important, and that he is willing to combine them with history, in the form of historical homology. But two further questions of clarification arise: Does he *also* agree that *selection* is important in classifying (historical) homologous traits? And does he also agree that *selection history* (i.e., what there was selection for, and not only what is apt for future selection) is? If he concedes all of this, the gap disappears. So we will assume that he

19. In fact, of the muscle fiber case, Neander asks just this, "which kinds of criteria—the functional or the structural—will become constitutive in this case?" She answers, "But this sets up a false dichotomy. The two are intimately interwoven and are more or less two aspects of the same thing" (2002, 408).

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does *not* concede at least the last, on pain of collapsing the distinction between the two views, and turning the dispute that remains into a merely terminological one.[20]

What is at issue in that case is the very role of *selection history* in trait classification. We maintain that many homologous types of traits are, constitutively, *types of adaptations*, whereas Griffiths is obliged to deny it.

Note, in making the claim that adaptation is important in homologous trait classification; we are not denying the importance of other things. In contrast, the proponents of the opposite view have denied that adaptation has *any* role in trait classification, outside of the analogous categories. Why take this extraordinary view? Why would *biologists*, who are after all so very concerned with adaptation and adaptations, among other things, *not* want a taxonomy of adaptations? We are not aware that any argument has been offered to persuade us that selection history is not present and operative in constituting categories of homologous traits. (Unless it is the contention that SE function is too inferential and non-observational.) The arguments that were originally offered, when the first sallies among the present parties were sent forth by Griffiths (1994) and Amundson and Lauder (1994), were merely arguments to the effect that most interesting biological classifications were homologous, as if this precluded their being functional, or at least SE functional. But their status as homologies leaves the role of selection history undecided, as we have argued. In contrast, we have offered a number of arguments for the classificatory indispensibility of selection history.

One powerful consideration is that the dispositions for which there has been selection, and the structures and mechanisms that are responsible for them, are of great biological significance. Dobzhansky's dictum—that nothing in biology makes sense except in the light of evolution, and more specifically in the light of Darwinian natural selection—might be an exaggeration but (without debating that) it holds more than enough truth for our present claim. If classifications are sensitive to the kinds of similarities and differences among traits that mattered in selection, they will thereby be sensitive to many of the kinds of similarities and differences that are important to biological theory, whether these be evolutionary, ecological, morphological, physiological or psychological. The task of classification is to carve nature at its most theoretically important joints, not just at any old joints; there are vastly too many of them for that, especially in the biological sciences. One main way that biologists do this, we claim, is by doing so directly, by carving at those places where—and

20. Confirmation of this attribution comes in a later paper, Griffiths 2007.

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because those places are where—there is a significant change in what there has been selection for.

A second consideration is less obvious and so we have taken some pains in this article to further articulate it. Not only does homology require prior specification of the trait in question, an inference to homology also often requires prior reasoning about adaptive pathways. It is often because a certain sequence in a proposed lineage makes adaptive sense that an inference to homology is justified. This speaks most directly to how we investigate the truth of homology claims, and less directly to the constitutive conditions for classification, which is the more immediate concern at this moment. However, it supports our contention that homology claims and SE function claims are both highly inferential, and interdependent, and so it undermines the counterclaim, which we take to be quite false, that homology is "manifest." There is no such reason to prefer an alternative approach that avoids the carving of nature at those places where—and because those places are where—there are significant changes in what there has been selection for.

A third consideration still turns on the significance of what Neander (2002) calls "abnormality inclusive categories." Since the dialectical ground has (at least as she sees it) shifted, the argument needs some recalibration. We have argued that similarity judgments, or at least specifications of the traits or characters judged to be homologous, are prior to homology claims. A resemblance in two separate species is regarded as homologous if it is derived from a common ancestor. But, as we know, traits or characters are not homologous simpliciter. Something is said to be homologous to something else *as a forelimb*, or *as a wing*, or *as a flipper*. Now let's consider how these specifications tell us in which respect two things are being said to be homologous. Suppose that two traits or characters in two separate species are homologous *as wings*. Is there, then, some resemblance that they share in virtue of being wings? Or suppose that two traits are homologous *as flippers*. Is there some resemblance that they share in virtue of being flippers? We do not assume that there must be a neat set of necessary and sufficient conditions, but there had better be something to say about it. We must then ask, What is a forelimb? What is a wing? What is a flipper? But this is, no less, and as we said above, a question about how traits are classified. We are now asking how traits are classified *as forelimbs*, and *as wings*, and *as flippers*. Our answer is, to say the least, very tempting here, at least for many biological classifications. Whether something is a wing or a flipper is, in part at least, a matter of its SE function.[21]

21. What of vestigial wings? It is constitutive of being a vestigial wing that the lineage

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But now suppose that someone tells us that there is no need for SE functions in classifying these traits as homologous, because causal-role function suffices (i.e., we can ignore selection history). It is hard to know what is being proposed precisely. Causal-role functions on their own do not suffice to classify wings as wings, and flippers as flippers, and esophageal valves as esophageal valves, and for well-worn reasons—because these classifications are abnormality inclusive. CR functions are actual causal dispositions, and some wings, flippers, esophageal valves, and so on, are abnormal and have abnormal causal roles. Some wings can and some cannot help a sparrow fly. Some flippers can and some cannot help a penguin swim. And some esophageal valves can and some cannot help us to move food through to and remain in the gut. Yet a sparrow's wing is homologous to a robin's *as a wing* even if it is broken.

One might attempt to give a prior specification of the traits in question in terms of their structural features, and we do not wish to rule this out as one strategy among others. However, just as some wings, flippers, and esophageal valves have abnormal causal roles, they can also have abnormal structures. The motivation for historical classifications of traits is akin to the motivation for having historical classifications of taxa, such as species. There are few purely ahistorical essences in biology.

We believe that, when we speak of two similar traits or characters in two separate species being homologous, we are ordinarily implicitly speaking of *normal* structural features and capacities. We are not merely speaking of actual structures or capacities (CR functions). Of course, congenital impairments can be inherited. And so there are lineages of such character traits as, e.g., hemophilia, which plagued the royal families of Europe for a few hundred years. Perhaps someone might want to say that the hemophilia of one royal male was homologous to the hemophilia of another. We see no great conceptual impropriety in speaking this way, but it is not typical homology-speak. Nor, to repeat, do we claim that typical homology-speak always refers to adaptations. We do not deny, for instance, that some "spandrels" are homologous to others. We repeat: ours is a pluralist position. We nonetheless maintain that many homologous types of traits are, constitutively, adaptations.

In those cases, the similarity judgments and the intraspecies trait classifications that are prior to homology claims will have to bring together both *normal*, properly working, and *abnormal*, defective and diseased instances of structures that vary along many topographic, morphological and compositional dimensions. As Darwin recognized, variation is the rule and not the exception, it has many sources and most variations are

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has had and then lost the SE function of flight, so SE function is still constitutively involved.

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deleterious. Such deleterious effects have causal-role consequences. What they retain, in the face of their abnormal causal roles and abnormal morphology, and sometimes in the face of their abnormal development, is a shared selection history. The role of a natural selection etiology in drawing the normal/abnormal distinction needed for correct judgments of similarity makes such judgments "essentially historical," in Neander's terms.

To classify something as either biologically normal or abnormal—by the by, a mode of classification in itself—requires that there be a standard of biological normality, and this is given, not by a statistical distribution, but by the solution to the design problem that created selection pressure on the lineage within which it figures.[22] Biologists, including and, perhaps, especially those concerned with questions of physiology, have a great many classifications of traits that more or less explicitly appeal to this distinction.

Griffiths grants the importance of abnormality inclusive categories. However, he counters, first, that "even if abnormality inclusive categories have to be 'essentially historical' this is no argument against their being defined by homology" (2006, 18). However, this misses the point since we do not deny that they are defined by homology. The question is what else is involved, because homology alone cannot suffice.

But there is a much more consequential oversight, according to Griffiths' second response to the claim that abnormality inclusive categories are "essentially historical." To show this he invokes the notion of developmental homology:

> 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 diseases process. . . . Neander's 'master argument' fails, and the need for abnormality inclusive categories can be met using homology. (Griffiths 2006, 18)

The question of whether there is a legitimate ahistorical (i.e., nonevolutionary) notion of homology cannot be treated in this article. However, Griffiths' appeal to developmental homology cannot show that homology is abnormality inclusive without presupposing selected effects, unless developmental homologies themselves are innocent of any selective effect presupposition. That they do often have such presuppositions is we think apparent in the role of developmental homology in grounding the

22. We take it that this is not in dispute by Griffiths, though it is disputed by some people.

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taxic homologies of inner ear, jawbone joint and gill arch expounded in Section 3. Recall, the crucial point there is that, as with taxic homologies, before a claim of homology can be made for a type of developmental structure, we need criteria of similarity to bring together a diverse set of topographies, compositions, and structures, as its instances. And that the kind in question is often constituted by the developmental structures' (SE) function—giving rise to diverse adapted characters.

6. Conclusion. Biology encompasses many different fields of specialization and there will be no one-size-fits-all formula for taxonomizing biological traits. We have therefore exercised some caution when it comes to making sweeping generalizations about how trait classifications are constituted. Though Dobzhansky's dictum—that nothing in biology makes sense except in the light of evolution, and more specifically in the light of Darwinian natural selection—is perhaps an exaggeration, it holds much truth. Natural selection, we all agree, sheds abundant light on how traits evolved. We maintain that it also sheds light on how traits are classified in theoretically interesting and useful ways. We conclude –still—that very many types of traits are types of adaptations, classified at least in part on the basis of their SE functions.

Objections to this view have taken different forms over the past several decades. In this article we defend it against those who argue that a combination of homology, morphology, and CR function can achieve the goals of biological classification, in the absence of considerations of past selection history. In closing, let us add that even if this claim were true, it would not show that our view was false, in so far as we claim that very many types of traits *are*, constitutively, types of adaptations, whether or not biology could or could not do without them. It would at most only show that they did not *need* to be used, in which case the parties to the debate about the nature of such classifications could call it a draw, at least for this round. However, we do not agree that a combination of homology and CR function, when divorced from considerations of past selection history, can achieve all of the same classificatory goals. The judgment that the same trait or two similar traits in two separate species is or are homologous often requires considering a chain of adaptation. And the claim that the same trait or two similar traits in two separate species is or are homologous always requires prior specification of the traits in question, a specification that cannot—for the abnormality inclusive categories—be done in terms of mere causal roles, for reasons we have explained.

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