

The Phenomena of Homologyⁱ

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Abstract

Philosophical discussions of biological classification have failed to recognise the central role of homology in the classification of biological parts and processes. One reason for this is a misunderstanding of the relationship between judgments of homology and the core explanatory theories of biology. The textbook characterisation of homology as identity by descent is commonly regarded as a definition. I suggest instead that it is one of several attempts to explain the phenomena of homology. Twenty years ago the 'new experimentalist' movement in philosophy of science drew attention to the fact that many experimental phenomena have a 'life of their own': the conviction that they are real is not dependent on the theories used to characterise and explain them. I suggest that something similar can be true of descriptive phenomena, and that many homologies are phenomena of this kind. As a result the descriptive biology of form and function has a life of its own - a degree of epistemological independence from the theories that explain form and function. I also suggest that the two major 'homology concepts' in contemporary biology, usually seen as two competing definitions, are in reality complementary elements of the biological explanation of homology.

1. Form, function, homology and adaptive function

"In the functional anatomist's vocabulary, form and function were both observable, experimentally measurable attributes of anatomical items (e.g. bones, muscles, ligaments). Neither form nor function were inferred via hypotheses of evolutionary history." (Amundson and Lauder 1994, 449)

In 1994 the functional anatomist George V. Lauder and the philosopher and historian of biology Ronald Amundson challenged the prevailing philosophical view that the parts and processes of organisms, the objects of study in anatomy and physiology, are defined by their adaptive function, that is, by the purpose for which they evolved (i.e. Millikan 1984, 2002; Neander 1991, 2002; Rosenberg 2001). Countless philosophy students have

been taught that the definition of the heart as ‘the organ whose purpose is to pump the blood’ is a typical example of biological classification. Amundson and Lauder remarked that this picture “is utterly false... [*as*] a glance in any comparative anatomy textbook rapidly convinces the reader” (1994, 453). In comparative anatomy the parts of organisms are primarily defined as *homologues*. The term ‘homologue’ was introduced in the early 19th century to denote “The same organ in different animals under every variety of form and function” (Owen 1843: 374)ⁱⁱ. Homologies are distinguished from *analogies* which are parts which resemble one another but are not instances of the same part. For example, the legs of human beings and the legs of birds are homologous, but the legs of human beings and the legs of insects are analogous. Since the late 19th century homology has most often been defined as resemblance due to common ancestry and analogy as resemblance due to parallel evolution, but as we will soon see, these definitions are not fully adequate.

Amundson and Lauder describe how in comparative anatomy descriptive evidence about the form of a part ("its physical shape and constitution") and about its function ("physical and chemical properties arising from its form") are used to support a hypothesis that it is homologous to a particular part in other organisms and/or a particular part elsewhere in the same organism (Amundson and Lauder 1994, 449). The primary identity of the part is the homologue of which it is an instance. Thus, for example, it was descriptive, and especially embryological, data which convinced biologists that the vertebrate skull is not composed of modified vertebrae, as was widely believed at the start of the 19th century. Instead, the skull is composed of bones such as the parietal, occipital, lacrimal, and quadrate, none of which are homologous to vertebrae. These bones vary greatly in form and function across living and extinct vertebrates, sometimes ossified, sometimes cartilaginous, often fused together in the adult and thus best identified by examining their form in the embryo. The idea that the small bones which form the cavities for the tear ducts in humans and the substantial, horn-like structures seen in the theropod dinosaur *Allosaurus* are both lacrimal bones because they serve a common evolutionary purpose is patently absurd. The fact that the bone is named functionally (*lacrima* = tear) is of merely

historical significance and no more implies that the bone is defined functionally than the name 'sonic hedgehog' implies that the gene *shh* is defined frivolously.

This is not to say that there are no biological categories defined in terms of selected function, as Amundson and Lauder themselves make very clear. Categories defined by selected function refer to 'analogues' – parts that have been shaped by a particular set of selection pressures (Amundson and Lauder 1994; Griffiths 1994; Griffiths 2006; Hull 1987). It is in this sense that both vertebrates and invertebrates have hearts, and also legs, heads, and wings. Consider the case of wings, which are found in two groups of living vertebrates (birds and bats), one group of extinct vertebrates (pterosaurs), and one group of invertebrates (insects). There is good reason to believe that certain distinctive features of these parts of birds, bats, pterosaurs, and insects are each the result of selection for flight, leading to the conclusion that these parts are all wings. However, the features of the four taxa that allow them to fly are not homologous to one another, no matter how similar they may be in adaptive function. In fact, the anatomical classification of the parts that make up the wing makes it clear that different parts have been adapted in each of these four, parallel instances of the evolution of flight. For example, because birds 'fly with their arms' while bats 'fly with their hands', the central ribs (rachises) of the primary flight feathers in the bird play a similar stiffening role to that played by the hugely elongated finger bones (phalanges) in the wing membrane of the bat - but this is no reason to classify the rachis as a variety of phalange! The bird's phalanges occupy their usual position in the overall plan of the vertebrate limb, although both the number of digits and the number of phalanges in each digit have been reduced during evolution.

In response to Amundson and Lauder's critique, Karen Neander has argued forcefully that the definitions of all biological categories nevertheless contain at least an implicit reference to adaptive function or evolutionary purpose. Rebutting Amundson and Lauder's claim that the ideas of function and structure employed in anatomy are straightforwardly descriptive, she asserts that:

“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” (Neander 2002, 414)

Debate continues as to whether there is always some implicit reference to evolutionary purpose in descriptive biological vocabulary (Griffiths 2006; Griffiths In Preparation; Rosenberg 2006; Wouters 2003, 2005, 2007), but whatever the verdict, the question remains why so many philosophers have thought it *obvious* that biological categories are defined by adaptive function. It is not all obvious that categories such as tibia and femur, duodenum and appendix, glial cell and platelet, blastula and notochord, ribosome and homeobox, cerebellum and pons, are defined by the adaptive purposes of these parts. It requires considerable philosophical argument to make this claim even plausible. At first sight each of these terms either names a homologue or is straightforwardly descriptive, reporting the observed form and function of the part.

Most of the philosophers who contributed to the old consensus view had no interest in comparative anatomy. This view of biological categories was formulated in the philosophy of psychology and only later applied to sciences such as anatomy (Millikan 1984; Neander 1983; see also Sober 1985). But a focus on psychological traits ought to have directed philosophical attention to neuroanatomy. The view that neuroanatomical structures are defined by their evolutionary purpose is implausible, because even the current function of many of these structures remains poorly characterised, let alone their evolutionary purpose. It might be suggested that one day, when the evolutionary origins of neural structures are fully understood, traditional neuroanatomical categories such as amygdala and insula will be replaced by new categories based on evolutionary purpose. But the actual practice of comparative neuroanatomy does not support this prediction. One of the most striking functional parallelisms in comparative neuroanatomy is that between the network of forebrain nuclei that allow the acquisition and production of birdsong and the network of language areas in the human brain. As a result of intensive research inspired by this parallel the neuroanatomical classification of the avian brain is undergoing extensive revision (for a review, see Jarvis 2005). Despite the fact that this research is inspired by the search for functional parallels, structures that have evolved

separately for the same purpose in songbirds and humans are not therefore identified as the same anatomical structure. Instead, avian neuroanatomists do what comparative anatomists have always done. They investigate the homologies of avian and mammalian brains as an essential backdrop to investigating the evolutionary analogies between them. To do otherwise would be to cripple the comparative method, perhaps our single most powerful tool for investigating the evolution of form and function (Griffiths 1996; Harvey and Pagel 1991). The comparative method allows us to study, amongst other things, how the form and function of the same part can diverge due to different selection pressures in different species, and how the form and function of different parts can converge due to similar selection pressures in different species. Collapsing the identity of a part with its adaptive purpose would merely obstruct these investigations.

Ruth Millikan and Karen Neander are both explicit about why they believe that biological categories must be defined in terms of selected function (Millikan 1984, 2002; Neander 1983, 1995, 2002). They think that descriptive categories, defined in terms of the actual observable properties of parts and processes, cannot unite normal instances of a character with abnormal instances, or exclude from a category items which coincidentally resemble the members of that category but do not, in fact, belong in the category. In earlier work I have pointed out that categories defined by common descent can, in fact, play this role perfectly well (Griffiths 1994; Griffiths 2006). A definition of the femur as all and only the bones which are copies by descent of a particular bone in the common ancestor of the tetrapods will include diseased and malformed femurs, and exclude bones that resemble the femur due to convergent evolution. This definition of the femur is, of course, merely an example of the conventional definition of a homologue. In this paper, however, I want to suggest that the popularity of the selected function approach to biological classification rests on a deeper and more philosophically interesting mistake than merely overlooking an alternative form of classification equally grounded in the theory of evolution. I have described how there seems to be an *a priori* tendency to suppose that descriptive categories, defined in terms of the actual observable properties of parts and processes, cannot provide an adequate basis for science and that biological categories must implicitly reflect a deeper, theoretically grounded classification. I suggest that this

reflects a failure to appreciate the nature of descriptive work in biology. Purely descriptive categories can embody deep insights into the structure of living systems independent of any links between those categories and the main explanatory theories of the biological sciences, whether natural selection or the theory of common descent. This failure to appreciate the epistemological independence of descriptive work from theory, I will argue, parallels the failure to appreciate the epistemological independence of experimental work from theory which was documented by the ‘new experimentalist’ movement in philosophy of science in the 1980s.

The epistemological status of homologues and analogues

“It would be hard to choose between function and homology as to which of them was more or less inferential or observational. In order to determine homologous relations, we have to make inferences about evolutionary history, just as we do when we determine normal [*adaptive*] functions.” (Neander 2002, 409)

Amundson and Lauder argue that comparative anatomists have used purely descriptive measures of form and function to provide operational characterizations of the parts of organisms that can serve as a relatively uncontroversial foundation for discussions of the ecological significance and evolutionary role of those parts. (Amundson and Lauder 1994, 449). While they do not actually describe homology as less inferential or more observational than adaptive function, they do think that assignments of homology are less epistemically demanding than assignments of adaptive function. In the quotation above, Neander points out that this appears inconsistent with the definition of homology as identity by descent. On this conception of homology, known as ‘Darwinian’ or ‘taxic’ homology, characters in different taxa are homologous if those taxa have the character by descent from a common ancestor. The taxic conception is associated with a particular method of identifying homologies, namely regarding characters as homologous if their distribution on a cladogram is consistent with their having originated only once in a common ancestor. The cladogram on which this judgment is based may be obtained independently of the character under study. In a particularly striking example, a

cladogram based on molecular data was used to reject the hypothesis that some neuroanatomical characters found in both large, fruit-eating bats (megachiroptera) and small, insectivorous bats (microchiroptera) are the result of convergent evolution, and to argue instead that those characters are homologous (Bailey et al. 1992). The more general case, however, is that in which a number of shared characters are used to estimate evolutionary relationships in a group of taxa. Individual shared characters are identified as either homologies or ‘homoplasies’ (non-homologous shared characters) depending on which view is consistent with the hypothesis of evolutionary relationships that is best supported by the entire set of shared character dataⁱⁱⁱ. It is notorious that homology diagnosed in this manner is an ‘inferential concept’ in the sense that more data may lead to a revised view of evolutionary relationships, and thus to a revised view of which shared characters are homologous and which homoplasious

Amundson and Lauder are both well aware of the inferential nature of taxic homology. In the discussion to which Neander is replying they have in mind an older, but still prevalent, approach to homology. Instead of inferring homology from a theory of evolutionary relationships, homologies can be diagnosed from descriptive anatomical data. The operational criteria used to diagnose homologies were developed by the highly successful comparative embryological tradition of the first half of the nineteenth century. Richard Owen’s definition of a homologue, “The same organ in different animals under every variety of form and function” (Owen 1843: 374), was given at a point where the theoretical basis of homology was exceedingly obscure. Owen himself offered a theory of ‘archetypes’, and his contemporary Karl Ernst von Baer explained homology in terms of shared developmental potentials in the egg. The inability to agree on a theory of homology did not prevent early 19th century biologists from developing the criteria of homology to the point where strong scientific consensus could be established on even subtle, distant homologies. Thus, well before Darwin dared announce his theory in public, some of the most powerful supporting evidence for that theory had already been established as biological orthodoxy. For example, Martin Heinrich Rathke had established the homology of the hyoid (hyomandibular) bone in tetrapods like ourselves and the second gill arch (hyoid arch) in jawless fish, and von Baer had identified the

notochord - the homologous structure that defines the chordates and from which the backbone develops in vertebrates. These investigators made much use of embryological evidence, which in the 19th century had something of the cachet that today attaches to molecular evidence. The particular value attributed to embryological evidence stemmed from von Baer's 1828 'laws' of development, a set of generalisations which even today retain considerable validity (but see Raff 1996). In essence, von Baer's laws state that the embryos of related species resemble one another more closely than do the adult forms of those species. As a result, the homologies of many parts are more apparent in the embryo than in the adult. To take a simple example, the embryonic primordia of two, separate structures in one species may fuse to form a single structure in the adult of a second species, but remain identifiable as separate structures in the embryo of that second species.

The operational criteria of homology used in the 19th century, and by Darwin himself in his massive comparative anatomical study of the *cirripedia* (barnacles), remain in use today, and were given a definitive modern statement by Adolf Remane (1952)^{iv}, who gives three principal criteria of homology. The first is the relative position of parts in the overall layout of two organisms. This criterion was implicit in the claims about homologies between bird and bat wings made in section one. The second principal criterion is the possession of 'special qualities', or shared features which cannot be explained by the role of a part in the life of the organism. The fact that in the vertebrate eye the blood supply to the retina lies between the retina and the source of light is a famous example of a 'special quality'. Remane remarks that the more complex a 'special quality' is, the better evidence it is for homology. The third principal criterion states that characters that cannot be homologised by the direct application of the first two criteria may nevertheless be homologous if they can be connected by a series of intermediates in other species such that each adjacent pair of characters can be homologised using the first two criteria. This idea of a homology not as a single, shared character state, but as a range of different states in which the same character can appear is sometimes referred to as a 'transformational' conception of homology. Remane also gave three auxiliary criteria of homology. Homologizing individual characters is part of a wider practice of

homologizing other characters and grouping whole organisms into taxa. The auxiliary criteria describe ways in which individual diagnoses of homology made using the principal criteria may be supported or undermined by judgments about the homology of other characters.

The insight embodied in Amundson and Lauder's discussion is that the operational criteria for judging homology carry a great deal of weight when compared to its theoretical definition in terms of evolution. In fact, there is good reason to suppose that the idea of homology is at least as tightly linked to the traditional operational criteria as it is to any theoretical definition of homology. The taxic conception of homology is therefore best conceived not as a definition but as an *explanation* of the *phenomena* of homology: the existence of 'corresponding parts' in organisms of different species is explained by their descent from a common ancestor.

In the next section I will provide some support for the claim that the concept of homology is tightly linked to the traditional criteria and that the taxic conception is not the only viable conception of homology. In the following section I will attempt to characterize in more detail the sense in which well-established homologies are 'phenomena'.

Homology and Theory

"By unity of type is meant that fundamental agreement in structure, which we see in organic beings of the same class, and which is quite independent of their habits of life. On my theory, unity of type is explained by unity of descent." (Darwin 1964 [1859], 206)

Following Darwin, common descent became the dominant explanation of homology. Some Darwinians proposed abandoning the term 'homology' and replacing it with a new term defined explicitly in terms of common descent ('homogeny', Lankester 1870). This proposal was not taken up, and the term 'homology' continued to be employed to denote characters identical by descent. The conception of homology as unity of descent, however, did not fit all the homologies which had been identified by comparative anatomists. In addition to taxic homologies, which he called 'special homologies', Owen

recognised homologies within the body of a single organism or ‘serial homologies’. The vertebrae in a single spinal column are (serially) homologous to one another, the corresponding bones in the forelimbs and hind limbs of a tetrapod are homologous, and each segment of an arthropod has parts homologous to the parts of other segments. Serial homologies are diagnosed in the same way as special homologies. The homologies between the bones in the human leg and those in the human arm are diagnosed using Remane’s criteria, just like the homologies between the bones in the human leg and the bones in the leg of a bird. The fact that serial homologies are not explained by the taxic conception of homology is no reason to think that they are illusions. It suggests, instead, that the fact that organisms descend from a common ancestor is not a complete explanation of the phenomena of homology.

The evolutionary developmental biologist Günter Wagner has argued that the taxic conception of homology is incomplete in a more pervasive way (Wagner 1989, 1994, 1999). It relies on the traditional criteria of homology to identify which part of a parent is homologous to which part of an offspring, but has no theoretical account of that relationship (see also Brigandt 2002). On the taxic conception, my arm is homologous to the wing of a bird because birds and mammals have a common ancestor that had forelimbs. Both arm and wing are copies of copies of copies of the same ancestral limb. Homology is thus defined recursively in terms of a relation of ‘copying’ between the parts of parents and the parts of offspring, but no account is given of this copying relation. Wagner argues that biology requires a ‘biological homology concept’ that would define homology in terms of the developmental mechanisms that generate correspondences between parent and offspring (for a similar view, see Millikan 1984, 19-25). In addition to plugging the hole in the taxic account of homology, the sort of developmental account of homology which Wagner envisages would provide a mechanistic explanation of the success of the traditional criteria of homology in identifying stable phenomena.

It is important to note that Wagner is not challenging the ability of biologists to successfully identify homologies so much as their ability to give a coherent account of

what they are doing when they identify them (Brigandt 2002). Biologists can identify putative homologies using the traditional operational criteria, or even fall back on the cruder approach of treating any shared character as a potential homology. Confidence that some shared character is a genuine homology can be generated by testing its congruence with other characters in the context of an attempt to work out the evolutionary history of life on earth. Patterns of evolutionary relationships that are suggested by many different character sets and which remain stable when new, unrelated data is added to the overall picture are probably real patterns. Empirical generalizations based on success and failure in using characters of particular kinds to find these evolutionary relationships can give rise to a purely empirical account of which characters are 'real' and which are either too evolutionarily labile to be useful, or too arbitrary to have any meaningful relationship to the evolutionary process (e.g. the ratio of the length of the tibia to the weight of the kidneys). The traditional taxonomist's intuitive sense of what is a 'good character' is presumably brute empirical knowledge of this kind. Nothing in Wagner's argument shows that such a purely empirical approach to homology is infeasible. However, the inability of this approach to give any theoretical account of the distinctions between 'real' versus arbitrary characters and 'real' versus illusory resemblances is clearly unsatisfactory. It leaves the Darwinian taxonomist in a worse position than Owen and von Baer, who at least had theories of homology which cohered with their other biological and metaphysical commitments. It is thus hard to disagree with Wagner that the taxic approach to homology is incomplete unless supplemented by a separate, mechanistic account of character identity.

One well-known proposal to solve the problem of character identity between parent and offspring, and simultaneously to explain serial homology, appeals to the idea of genetic information (Roth 1984; van Valen 1982). The corresponding parts of parent and offspring are those that express the same genetic information, and serial homologues are repeated expressions of the same genetic information. But the definition of homology as continuity of biological information is best regarded as a promissory note for a developmental homology concept. In our present state of knowledge the only operational version of this proposal would define homology in terms of continuity of the genes

expressed in the ontogeny of the trait and this is clearly inadequate. Traits that are not homologous can be built from the same genes and homologous structures can be identified even when the genes involved in the relevant developmental pathways have been substituted by evolutionary change^v. In a recent paper, Wagner has speculated that the key to explaining the persistence of morphological homologues across evolutionary time may be to look, not for homologous genes, but for evolutionarily conserved portions of gene control networks (Wagner 2007). While Wagner's new proposal does not explicitly make use of the idea of biological information, it has a definite affinity with accounts which do, looking to find constancy in the molecular mechanisms that build homologues. But whether or not this particular approach succeeds, "...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 and see Brigandt, this issue.). In other words, the main goal of a developmental approach to homology is to explain the phenomena of homology.

While the developmental account of homology envisaged by Wagner has yet to be developed for morphological characters, something like it exists for homologies between biomolecules (Brigandt 2002). Molecular biologists have developed their own vocabulary for discussing homology. When DNA sequences or the molecules derived from them are taxic homologues of one another, that is, derived from a common ancestor as the result of organisms reproducing themselves in the usual ways, molecular biologists call them 'orthologues'. They call DNA sequences and the molecules derived from them that are serially homologous with one another, that is, which occur in multiple copies in a single genome as a result of gene duplication or genome duplication events, 'paralogues'. They call DNA sequences that have entered a genome by lateral transfer from the genome of a different species 'xenologues'^{vi}. The difference between the molecular and morphological levels is that in the molecular case, when we say that two DNA sequences are both copies of a single ancestral sequence we know exactly what we mean by 'copy'. For example, the genome of bread wheat is a hexaploid derivative of the hypothesised ancestral crop grass genome whose nearest extant representative is the rice genome

(Devos and Gale 2000; Gale and Devos 1998). The homologies (orthologies) between the wheat and rice genomes can be diagnosed using the molecular equivalent of Remane's criteria. Most important amongst these is the first principal criterion, relative position, which in this case means the linear order of the sequences on the chromosomes. In line with the recommendations of Remane's auxiliary criteria, biologists have used the highly conserved order of sequences in specific chromosome segments to homologise whole chromosomes and larger segments of chromosomes, discovering by this means various inversions and translocations of chromosome segments during the evolutionary history of the crop grasses. The homologies (paralogies) between different sections of the wheat genome which represent the different copies of the ancestral crop grass genome that have been generated by whole-genome duplication have been diagnosed in the same manner. The various molecular-level causal processes that are postulated in this account of the homologies of the crop grasses are all well-documented in living organisms – normal genome replication, including the inversion and translocation of chromosome segments, gene duplication, and whole genome duplication leading to polyploidy. The molecular mechanisms by which these processes occur are sufficiently well understood that we can claim a mechanistic understanding of why these genomes exhibit such striking homologies to one another.

When we understand the replication of bodies and behavior to some thing like this level of detail, we will have the developmental account of homology that Wagner envisages. In particular, we need to understand why morphological structures and processes retain their identities across evolutionary time in a way that is to some degree independent of the identity of the specific genome sequences that are involved in their ontogeny (Wagner and Misof 1993 and see fn. 5). Developmental explanations of homology will not displace explanations in terms of common descent, since the two are strictly complementary elements of a complete explanation, at least in the case of taxic homology. Moreover, it seems quite possible that when the processes that generate homologies are fully understood, morphological homology may be subdivided into different, process-based categories, in the same manner as molecular homology.

What philosophical lessons can we derive from these recent disputes about homology? First, proposals to redefine homology use specific judgments of homology based on widely accepted operational criteria to contest the theoretical definition of homology. This is evidence that judgments of homology have a degree of epistemic independence of the theories that explain homology. Second, as we saw in the case of molecular homology, a successful explanation of some homologies may lead to the ‘rigidification’ (Kripke 1980) of the term homology so that it refers only to phenomena that can be explained in this manner. But this does not lead to the remaining homologies being dismissed as illusions. Instead, they remain as separate phenomena in need of a separate explanation. In the next section I will try to give some more substance to the idea that many homologies are robust phenomena that stand in need of explanation and whose reality is to some extent independent of current theory.

The phenomena of homology

“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.” (Griffiths 2006, 10)

In the last section, I mentioned the extensive homologies between the genomes of crop grasses such as rice, wheat, and millet. The same genes are found in the same linear sequence in these different species despite major differences in the number and gross structure of chromosomes. If the genomes of these organisms are drawn as a series of concentric circles, each circle representing the genome of one species, then by relocating a relatively small number of chromosome segments a diagram can be produced in which a line drawn from the centre passes through the same gene in each of the circles (Devos and Gale 2000; Gale and Devos 1998). Once such a diagram has been constructed, the position of genes in a circle representing a genome which has not been finely mapped can be reliably predicted from their position in the other circles representing genomes which have been finely mapped. This phenomenon (sometimes referred to as ‘synteny’^{vii}) is a

striking fact that exists quite independently of the theory of descent with modification, which confirms that theory, and which a creationist or other sceptic must seek to explain in some other way.

A similar class of scientific facts inspired an important development in the philosophy of science in the 1980s. The 'new experimentalists' questioned the view that the content of science consists only of successful, explanatory theories (Franklin 1986, 1990; Hacking 1981, 1983; Mayo 1996). They argued that scientific work is at least as much about creating new phenomena as it is about creating theories that explain phenomena. Experiments are not conducted only to test theory, but also as a way of exploring nature in their own right. An 'experimental tradition' can possess its own momentum, moving ahead independently of theory, and leaving theorists to catch up with the new phenomena that have been created. The two aspects of 'new experimentalism' that concern me here are 1) the idea that there can be good reasons to accept the reality of experimental phenomena independent of theory and 2) the idea that an experimental tradition can make substantial contributions to scientific knowledge in its own right, and not only by confirming or disconfirming theories

The first of these ideas can be found in Ian Hacking's classic discussion of microscopy (Hacking 1981). We have good reason to accept the reality of many microscopic observations independent of the theories that explain the workings of microscopes. The same phenomena may be observed through microscopes which work on very different principles, such as simple versus compound optical microscopes. An object at the limit of resolution for the naked eye may be mechanically reduced in size, and then viewed through the microscope to see whether the apparatus reproduces it veridically. These arguments for believing what is seen through a microscope do not appeal either to the kinds of theories we use microscopes to test or to the theory of the working of the microscope. Instead, they provide direct, independent, reasons to accept the reality of the phenomena observed with the microscope.

It is worth noting that although microscopy is treated in the literature as an example of the creation of 'experimental phenomena', the microscopists manipulation of their materials is for the most part not intended to create new phenomena, but to render existing natural phenomena observable. Robert Brandon has argued that there is a continuum between experiment and observation, depending, amongst other considerations, on the degree to which nature is manipulated to produce a phenomenon (Brandon 1994, 61-65). If we adopt this model, then biological 'description' seems to involve as much experimentation as it does observation.

What are the equivalents in the case of homology of Hacking's direct, independent arguments for the reality of microscopic phenomena? They are primarily matters of consilience between observations in one species and those in another. For example, in the early days of comparative anatomy homologies that were hard to decipher in one species, such as those between the embryonic and mature states of the human urinary-genital system, were successfully resolved by examining homologous parts in other species. If the use of the comparative approach had led investigators astray, rather than leading to breakthroughs in understanding the target system, this would have thrown doubt on the reality of the homologies on which they relied. Or consider what is often referred to as the 'theory' of the vertebrate skull (a usage we will return to below). This 'theory' is simply the claim that all vertebrate skulls can be modelled as transformations of a general plan consisting of a specific set of parts and a specific set of relations between those parts. The theory is confirmed by the fact that the skulls of new vertebrate species can be reduced to the same plan. It is most strongly confirmed by cases which initially appear not to fit but can be made to fit by investigating them more closely (for example, by finding that what appears to be one bone is a fusion of two embryonic precursors). In a highly developed account of a class of morphological structures such as this, the names of homologues are 'entrenched predicates' in Nelson Goodman's (1954) sense. A history of success in using these predicates in a wide range of inductive inferences provides grounds for supposing that they taxonomise the phenomena in a way that corresponds to actual causal processes in nature.

A second idea that can be derived from the ‘new experimentalism’ and applied to the case of homology is that an experimental tradition accumulates knowledge in its own right, not merely by confirming theories. However, the traditional view of description which this new view throws into question is not an exact parallel to the traditional view of experiment which was questioned by the ‘new experimentalists’. Experiment was traditionally seen by philosophers of science as something which follows on from theory. An experimental tradition was conceived as a series of tests of a theoretical framework, the framework being revised when necessary in response to the results of experiment. The new experimentalists argued that nature can be explored by pursuing an experimental tradition in its own right, for example, exploring the range of conditions under which certain effects can be reproduced, or learning to recreate a natural phenomenon under controlled laboratory conditions. Experiment, they argued, can precede theory. In contrast, traditional models of science have not denied that description can precede the development of the theories that explain what has been described. But while allowing that this can occur, the traditional picture has downplayed the scientific significance of the descriptive phase. ‘Describing’ the vertebrate skeleton was not a matter of merely dissecting and recording what was seen, but involved advancing hypotheses, testing them out in new taxa, developing new techniques that allowed specimens to be prepared in such a way as to carry out these tests, and revising the account of the skeleton so as to cope with anomalies whilst still accommodating the mass of existing data. A striking modern example can be found in work on the homologies of avian digits (Müller, Gerd B 1991; Müller, Gerd B. and Alberch 1990). Birds have only three, much reduced digits. Paleontological data can be used to support the rival hypotheses that these are homologous to either digits 1-2-3 or digits 2-3-4 in other vertebrates. Experimental evidence, however, suggests strongly that the second hypothesis is correct. Digits form from cell condensations in the limb bud. The evolutionary loss of digits reflects a change in the number of condensations in the early stages of limb development. In several taxa, including crocodylians which are the nearest living relative of birds, the developing limb bud has been subjected to experimental treatments which inhibit the formation of cell condensations. These studies show that more or less severe inhibition affects the formation of cell condensations in the order 1-5-2-3-4, the reverse of the order in which

the condensations form in normal development. This suggests that birds have digits 2-3-4, not 1-2-3. Here we have a principled, mechanistic and evolutionary answer to the question 'which digit is which', a question that someone who did not understand homology might be inclined to regard as a matter for stipulation. Ofer Gal has suggested to me that the kind of biological work represented by vertebrate morphology is akin to the work in astronomy that led to the formulation of Kepler's laws of planetary motion. There is a sense in which Kepler's discovery that, for example, planets sweep out equal areas in equal times was merely a description of what happens. But it was also a scientific achievement of the first magnitude.

Thanks to the writings of the 'new experimentalists', the creation of novel phenomena in the laboratory, famously exemplified by Faraday's series of discoveries in electromagnetism, is now recognised as a critical component of scientific activity. But to date it has not been recognised that a major work of scientific description, such as the 'description' of crop grass genomes, or the 'description' of the vertebrate skeleton can play the same role. To 'describe' something in this sense is to engage in a sustained program of research that results in a principled and reproducible way of characterising and classifying objects of that kind. So it is no great step from the idea that experiment has a life of its own to the idea that description has a life of its own. The results of a descriptive research program can run ahead of the capacity of current theory to explain phenomena and set the agenda for future theoretical work. Contemporary genomic research provides just such an example. It is a truism that in 'postgenomic' molecular bioscience, explanatory theory is playing catch-up with the output of a massive program of descriptive work, including mass sequencing, genome annotation and comparative genomics. This situation is usually said to have arisen because biology lack tools to deal with the sheer volume of data from those descriptive endeavours. But while this is undoubtedly true, it is also misleading. The genomics revolution did not merely flood biologists with more of the data they were familiar with from the classical period of molecular biology. In fact, rather than discovering an unmanageable number of protein-coding genes, whole genome sequencing and annotation has revealed that there are far fewer than was previously supposed. Several new, unsuspected classes of small RNAs

have been discovered, and these seem to play a critical role in the molecular biology of the cell (Mattick 2003, 2004). The variety of ways in which molecules have turned out to be synthesised from the genome has led many to conclude that a purely structural definition of 'gene' is no longer possible (Griffiths and Stotz 2007; Snyder and Gerstein 2003). In these and other ways descriptive genomics is running ahead of biological theory and setting the agenda for theory building.

It is possible that the many new phenomena discovered by postgenomic molecular biology will one day be explained by a set of abstract, mathematical principles in the way that the electromagnetic phenomena discovered by Faraday were explained by Maxwell's equations and classical field theory. At the present time, however, the only principles that resemble traditional laws of nature in molecular biology are those imported wholesale from chemistry and physics (Weber 2005). Molecular bioscience itself does not discover new, higher level laws, but instead discovers molecules and mechanisms, such as the various classes of small RNAs mentioned above. Major discoveries take the form of molecules and mechanisms which are ubiquitous and which help explain core cellular functions. In an attempt to make philosophical sense of this kind of science Rasmus Winther (2006) has argued for a distinction between two forms of biological theory. Disciplines of 'formal biology' like population genetics are structured around an abstract, usually mathematicised, theory comparable to those seen in the physical sciences. General knowledge about the objects of study of these disciplines takes the form of confirmed theories. Particular facts are explained by applying these theories. In contrast 'compositional biology' disciplines like anatomy, physiology, developmental biology and molecular biology are structured around an inventory of parts and processes. General knowledge about the objects of study of these disciplines takes the form of a privileged ontology of parts and processes whose reality and properties have been confirmed in the manner laid out above. Explanations take the form of documenting particular mechanisms in which these parts and processes are actors (Craver and Darden 2005; Machamer et al. 2000). In the case of anatomy, physiology and developmental biology, I would argue, these actors are parts and processes defined by homology.

In this section I have tried to sketch a sense in which homologies can be robust phenomena with a degree of independence of explanatory theories in biology. I have suggested that we have direct grounds for accepting the reality of certain homologues, so that like robust experimental phenomena they have a degree of epistemic independence from the theories that are used to explain them. Of course, these direct arguments are defeasible, and the arguments vary in strength from case to case, but exactly the same is true of experimental phenomena. I have also suggested that in such cases ‘mere description’ is an important and demanding form of scientific activity.

Conclusion

I have tried to place the difficulty that philosophers have had in assimilating the central role of homology in the classification of parts and processes in biology in a broader context. It is another example of the overly exclusive emphasis on theory in the philosophy of science. It has been assumed that principles of classification that can unify diverse particulars into broad categories that can form the basis for future scientific work must be derived from our best explanatory theories of the domain to be classified. I have argued instead that description, like experiment, has a ‘life of its own’. Descriptions can be scientific achievements of great significance, and we can have good reasons to accept the reality of phenomena that have been described in the absence of any theory that explains those phenomena. Descriptive phenomena supported by the kinds of considerations I have outlined have a degree of epistemic independence from theories that purport to explain them – they cannot be dismissed as illusions merely because current theory fails to make sense of them. Instead, as Ingo Brigandt (2003b) has argued in the case of species, robust descriptive phenomena provide the agenda that theory must either explain or convincingly explain away.

An important consequence of viewing homologies as robust descriptive phenomena, is that the competing concepts of homology found in the biological literature, are revealed to be complementary aspects of an explanation of these phenomena, and not the competing theoretical definitions that much of the existing literature takes them to be.

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ⁱⁱ While I believe that picture of the role of the homology concept in biological thought I give here is broadly accurate, for reasons of space my treatment of the history is sketchy in the extreme. For more detailed and no doubt more accurate accounts, see (Camardi 2001; Gilbert 1991; Lenoir 1989; Maienschein and Laublicher 2007; Richards 1992; Williams 2004), on all of which I have drawn freely. The same constraint prevents me giving a full account of the recent biological literature on the homology concept, and on character identity more generally, for which see (Bock and Cardew 1999; Hall 1994, 2003; Hall and Olson 2003; Wagner 2001). For recent specifically *philosophical* work on the homology concept, see (Brigandt 2002, 2003a, 2006; Griffiths 2006; Love 2001, 2007; Matthen 1998, 2000) and the other papers in this issue.

ⁱⁱⁱ For a thorough philosophical treatment of this kind of phylogenetic inference, see (Sober 1988).

^{iv} For an English translation, see (Riedl 1978) For historical treatments of early 19th century comparative anatomy, see references in footnote 1.

^v Examples are given in my (2006). For discussions of this important topic of 'levels of homology', see Brigandt, this issue; Love, this issue, Ereshefsky, this issue, and the biological works cited in footnote 1.

^{vi} Xenology has no real morphological counterpart, although the sharing of heritable endosymbionts in some ways resembles xenology.

^{vii} This usage remains controversial because 'syntenic' also means 'physically located on the same chromosome'.