Homology and Homoplasy: A Philosophical Perspective

Introductory article

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Homology refers to the underlying sameness of distinct body parts or other organic features. The concept became crucial to the understanding of relationships among organisms during the early nineteenth century, and it remains important today. Definitions of homology have changed with the progress of biology, and even today different versions are associated with different research agendas. The differences illustrate philosophical issues about the workings of definition and explanation in science.

Article Contents

The Concept of Homology up to Darwin

The organic world is amazingly diverse, but patterns of unity can be seen throughout it. Evolutionary biology has the double task of accounting for both the diversity and the unity of life. These two aspects are tied to the two most central concepts in evolutionary theory: adaptation and homology. Adaptive radiation is believed to account for the diversity of life forms. Relations of homology express their unity.

Homology is sameness, judged by various kinds of similarity. The recognition of body parts that are shared by different kinds of organisms dates at least back to Aristotle, but acceptance of this fact as deeply important to biology developed during the first half of the nineteenth century. In an influential definition published in 1843, Richard Owen defined homologues as 'the same organ in different animals under every variety of form and function'. Owen had a very particular kind of structural sameness in mind. It was not to be confused with similarity in function, which was termed 'analogy'. Bird wings are not homologous to insect wings even though they look similar and perform the same function. Because the similarity is ascribed to functional need, they are identified as analogues. On the other hand, the wings of birds, the front fins of porpoises, the forelegs of horses and the arms of humans are all homologous. Even though they look different and function in different ways, they are the same in the sense of homology. Some body parts bear very little resemblance to their homologues in other species. The incus and malleus, tiny ear bones in mammals, are homologous with the bones that form the jaw joint in reptiles. A distinct but related concept that Owen called serial homology identifies repeated elements within an individual organism. All of the vertebra in an individual's body are serial homologues, as are their right and left limbs. An interesting pre-Darwinian discovery of serial homology was the identification of the parts of flowers (petals, sepals, etc.) with the leaves of plants.

A heated biological debate during the early nineteenth century concerned the relative importance of the principles of unity of type versus conditions of existence. Unity of type expressed the consistency of generalized categories (Types) that reflected the organization of nested sets of homologies. Owen, for example, proposed the vertebrate archetype as the generalized form of the vertebral skeletons, and sometimes spoke of the archetype as an abstract platonic idea. Conditions of existence expressed the diverse adaptations of organisms to their environment and internal physiological needs. This contrast shows that the dual importance of homology and adaptation predates evolutionary thought. Some recent scholars have attributed the anti-evolutionism of the early nineteenth century to the mystical 'typological thinking' of the unity of type advocates. In fact the typologists were very diverse in their views on metaphysics and on evolution. They ranged from mystical to materialistic and even included T. H. Huxley, Darwin's strongest supporter. Typologists were united not by metaphysical or anti-evolutionary commitments, but by a belief in the importance of homology over adaptation.

One of Darwin's great successes was his use of the well-established facts about homology as evidence for common ancestry. Darwin rhetorically transformed Owen's archetype into an ancestor, and showed how nested sets of homologies are just what we would expect from genealogical relationships. Darwin considered 'the homological argument' among his best evidence for evolution.

The Historical Definition of Homology

Darwin accepted the patterns of homology discovered by unity of type advocates as data that could be explained by the fact of common descent. His transformation of the archetype to an ancestor gave a more concrete explanation for homological patterns than the types and archetypes of earlier thinkers. The Darwinian E. R. Lankester argued in 1870 that the old definitions of homology and analogy should be abandoned because of their association with outmoded idealist concepts like Owen's. His replacement term (homogeny) never caught on, but its definition did. Lankester defined homogenous characters as those that 'have a single representative in a common ancestor'. Lankester's definition (of homogeny) has become the most common modern definition of homology: 'A feature in two or more taxa is homologous when it is derived from the same (or a corresponding) feature of their common ancestor'.

Lankester introduced the term homoplasy to designate shared similarities that were not traceable to the most recent common ancestor of two species. Homoplasy is thus broader than analogy, because the similarity can come from any source other than recent common descent (including both functional adaptation and mere accident, selection or genetic drift). Evolutionists are these days somewhat cautious about identifying features as adaptive, an identification that would be necessary in order to determine that body parts are analogous. Partly for that reason the more general and cautious term homoplasy has become widely used.

Criteria versus Definitions

The recognition of particular homologies cannot be based on the historical definition, for various reasons. For one thing, the same homologies were recognized by pre-Darwinian, nonevolutionary biologists as by evolutionists. For another, the best evidence we have of common ancestry is homology itself! If we cannot know about common ancestry without discovering homologies, then we cannot use common ancestry as a recognition criterion for picking out homologies. This apparent circularity is sometimes used to criticize the historical definition. If common ancestry defines homology, then we cannot know whether a similarity is homologous without knowing common ancestry. But homologies are our only way of inferring common ancestry. Therefore in order to recognize traits as homologous we must already know they are homologous!

This criticism relies on a faulty view of what scientific definition amounts to. A scientific definition is not a semantic stipulation that creates an analytically true statement (i.e. a statement the denial of which is self-contradictory). Rather, a scientific definition typically states a property that is considered to be the most deeply explanatory of the phenomena that are central to the term being defined. Lankester and Mayr consider ancestry to explain patterns of homology, and stress that fact by making it the definition. The historical definition is not viciously circular as long as homologies can be recognized and picked out by criteria other than common ancestry. It is an empirical fact that homologies (as picked out by the criteria below) are arranged among organisms in a pattern that is explainable by common ancestry, and independent evidence from various fields supports common ancestry as a historical fact. As we will see, those who differ in their theoretical interests can also differ in their definitions of homology.

Most of the criteria used for recognizing homologies have changed little since pre-Darwinian days. An important criterion is the principle of connections originally articulated by Geoffroy Saint-Hilaire. Homologous body parts might differ greatly in shape and even composition, but can be recognized by their topological connections to the body parts around them. A second criterion is the embryological origin of a body part. Body parts that differ in adults are sometimes observed to develop out of the same parts in early embryos. Embryology allowed the discovery of the ear bone/jaw bone homology above. Here the homological sameness is inferred from the similarity of topological connections even thought the bones themselves are very dissimilar. A third traditional criterion is the existence of transitional forms of the character in adults of related species.

Criticisms of the Historical Definition

The historical definition is subject to criticisms in addition to the unsuccessful charge of circularity. It appears more concrete than Owen's definition because a real entity (an ancestor) rather than an ideal archetype is named as the source of the homologues. But in fact it is vague in precisely the way Owen's definition is. What exactly constitutes sameness? The historical definition defines the sameness of two contemporary homologues (say a bird's wing and a whale's fin) in terms of the sameness each of them bears to the part body of an ancestor (a reptile's forelimb). But this only pushes the problem back. What constitutes the sameness of the wing with the ancestral forelimb? We sometimes speak loosely of birds' wings having descended from dinosaur forelegs. But this is truly nonsense – body parts do not descend from other body parts. Each organism grows its body parts anew during embryogenesis. The historical definition does successfully explain why the pattern of homologies is a nested hierarchy rather than some other pattern. But it does not, any more than Owen's definition, explain what 'same' means. Lankester speaks of homologies being represented in, and Mayr speaks of them corresponding to body parts of a common ancestor. Representation and correspondence are merely synonyms for sameness.

If we agree that patterns of homology reflect patterns of ancestry, the historical definition of homology adds nothing more. The increased interest in homology in recent years has arisen from developments within two specialized disciplines related to evolutionary theory. One is the area of systematics and the rise of cladist taxonomic methods. Cladistic methods provide much more rigorous standards for constructing phylogenetic trees than do traditional evolutionary methods. The second is developmental biology and the recent increase of interest in development as related to evolution theory.

Taxic and Developmental Definitions

Cladist taxonomists have introduced the concept of taxic homology. Homologies are identified with synapomorphies, features that are shared among species and derived from an ancestral species. The important point is that synapomorphies are not discovered by inspecting the candidate features alone. Rather, synapomorphies are determined by considering all known features of a group of organisms and constructing the phylogenetic tree that explains the distribution of features by assuming the fewest evolutionary character changes. This introduces a test of homology in addition to the traditional ones. Purported homologues must be distributed among species in a pattern that is congruent with the distribution of other traits. Both Owen's and the historical definition of homology were based in comparative anatomy rather than systematics. No one from Owen on would knowingly have proposed homologies that violated known patterns of character distribution, such as homologizing the eyes of octopuses and mammals. But this principle was implicit rather than explicit. The taxic definition places the systematic requirement for monophyletic trees at the centre of consideration, with anatomical considerations such as connections and embryological origin being secondary. The new, rigorous cladistic requirements for hypothesizing common ancestry draw attention away from the anatomies of individual characters and their transformations.

The developmental definition directs attention back towards anatomy, and especially towards embryology. The crucial feature of homologues, on this view, is their ontogenetic development. The historical and taxic views of homology treat homologues as causal byproducts of the history of evolutionary diversification. They are evidence of past unities – the unity of the common ancestor of now-diverse groups. But homologies are epiphenomena, causal byproducts not causal actors, in the current world. Many developmentalists disagree. They see homologues as indicators of the commonness of the developmental processes that give rise to them. A central doctrine of the new programme of evolutionary developmental biology 'Evo Devo' is that phenotypic evolutionary change can only take place by changes in the genetic and epigenetic processes that generate phenotypes. Evo Devo practitioners study developmental processes that are common to taxa of various ranks, and believe that this knowledge will contribute to understanding evolution. Defining homologies in terms of embryological commonality draws attention to the shared elements of those developmental processes. This means that homologies (developmentally defined) are closely tied to contemporary causal processes, namely the processes of embryogenesis and development. They are not mere epiphenomena, as they appear under the historical and taxic definitions.

One significant problem for the developmental definition is the now well-known fact that homologous body parts (identified by anatomical and historical/taxic criteria) do not always develop from identical embryological processes. Early development is to some extent decoupled from adult phenotypes through their evolutionary history, so that early ontogenies are free to vary. This refutes some versions of developmental definition, such as V. L. Roth's requirement that homologies share developmental pathways. On the other hand, some ontogenetic process or other must be responsible for the persistence of adult characters in the face of the flexibility of the events that bring them about. Günter Wagner proposes to define homologies in terms of shared developmental constraints. These constraints can account for the persistence of adult characters in the face of variation in their developmental pathways. This approach maintains a focus on developmental origins, but also allows a conceptual interface with variation and natural selection, since developmental constraints are constraints on variation. This is not the only use of the concept of developmental constraints within Evo Devo. The research programme considers bauplans (or body plans) to be robust, persistent features of the history of life on Earth. Bauplans are identified as sets of extremely deep homologies. Developmental constraints play a role in explaining the persistence of bauplans independent of their proposed role in defining homology.

Differences in theoretical orientation affect a scientist's favoured definition of homology. Many evolutionists reject the Evo Devo claim that the persistence of bauplans is a phenomenon in need of explanation. For them homology is an epiphenomenon, merely the residue of common ancestry. If this is so, the historical or the taxic definition explains everything worth explaining about homology: the branching hierarchy of residual characters. Supporters of the developmental definition consider bauplans and homology to depend on developmental factors beyond the mere sharing of ancestry. The phylogenetic persistence of homologies and bauplans, and the particular characters that are conserved require explanation. An explanation of the branching pattern is not enough.

Inconsistent or contrasting definitions may seem paradoxical, but they are not unusual in science. The concept of the gene varies greatly between research programmes, and the concept of adaptation is defined differently by those with different theoretical orientations. Homologies among DNA sequences are now discussed, and advances in developmental genetics have stimulated proposals of other new kinds of homology, such as homologies of developmental processes rather than the traditional anatomical items. Some of these variations are due to the hierarchical organization of life itself, others to substantive differences in biological theory. It is unlikely that a unitary definition of homology will be settled on anytime soon. The sameness expressed by homology has a different sort of importance to population biologists, to taxonomists, and to developmental biologists.

Further Reading

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