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Homoplasy and homology: Dichotomy or continuum?

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Abstract

Homology is the presence of the same feature in two organisms whose most recent common ancestor also possessed the feature. I discuss the bases on which we can tell that two features being compared share sufficient elements of sameness to allow them to be treated as homologous and therefore to be legitimately compared with one another in a way that informs comparative, evolutionary, and phylogenetic analysis. To do so, I discuss the relationship(s) between homology and homoplasy to conclude that we are dealing neither with a dichotomy between homoplasy as parallelism/convergence and homology as common descent nor with a dichotomy of homoplasy as the interrupted presence of the character in a lineage and homology as the continuous presence of the character. Rather, we are dealing with common descent with varying degrees of modification. Homoplasy and homology are not dichotomies but the extremes of a continuum, reflecting deep or more recent shared ancestry based on shared cellular mechanisms and processes and shared genes and gene pathways and networks. The same genes can be used to initiate the development of homoplastic and homologous structures. Consequently, structures may be lost but their developmental bases retained, providing the potential for homoplasy. It should not be surprising that similar features persist when a feature is present in the nearest common ancestor (homology). Neither should it be surprising to find that different environments or selective pressures can trigger the reappearance of similar features in organisms that do not share a recent common ancestor (homoplasy).

Keywords: Homoplasy; Homology; Convergence; Parallelism; Similarity; Common descent

Introduction

Those who know my work will know that I could not by any stretch of the imagination be described as an anthropologist—social, physical, cultural, or any other variety. I do, however, share with many of my anthropologist colleagues a long-time interest in one of the central problems that anthropologists—indeed that any comparative biologist—must tackle on a day-to-day basis in their research. That problem is homology (for recent evaluations, see Hall, 1994, 1995, 1998, 2003, 2006; Bock and Cardew, 1999).

A working definition of homology is the presence of the same feature in two organisms whose most recent common ancestor also possessed the feature. Homologues therefore share an ancestry, which either may be shared ancestry of the feature itself or sharing ancestors that display the feature—we are often not explicit about the level of shared ancestry being compared. How do we know that two features being compared share sufficient elements of sameness to allow them to be treated as homologous and therefore to be legitimately compared with one another in a way that informs comparative, evolutionary, or phylogenetic analysis? An important component of the answer to this question is how we identify homologues and, consequently, how we identify the class(es) of features that represents the obverse, or absence of homology (the dichotomy of the title), or perhaps, how we set the limits of a set of continuous processes (the continuum of the title).

Features that are not homologous are usually regarded as analogous (Boyden, 1943; Hall, 1994). Consequently, for most biologists and anthropologists, analogy is the antithesis or inverse of homology. As discussed by Panchen (1994), the distinction between homology and analogy was recognized

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even before Richard Owen distinguished them in terms that still apply today:

> Homologue … the same organ in different animals under every variation of form and function… Analogue … a part or organ in one animal which has the same function as another part or organ in a different animal (Owen, 1843: 379, 374).

Homology versus analogy is the dichotomy or antithesis that most would propose if required to state the antithesis of homology.

There is, however, a third way of comparing structures/characters among organisms, and that is *homoplasy*, a term introduced by Lankester (1870) for phenotypic similarity resulting from independent evolution. Like Lankester, indeed, in the same year, Gegenbaur (1870) also saw the need to invoke evolutionary ancestry when assessing homology, although earlier, Gegenbaur (1859) followed Owen (1843, 1848) in relating homology to types.

Concerned that the term homology was loaded with too much Platonic idealism and was too closely associated with types and archetypes, Lankester distinguished two classes of similarity on the basis of shared versus independent evolutionary history and proposed two new terms for them:

- *homogeny*—features shared by two organisms and present in their nearest common ancestor—similarity due to common descent; and
- *homoplasy*—other resemblances involving convergent evolution—similarity arising from independent evolution.

The term homogeny did not take hold. Instead, definitions of homology changed to incorporate the essential element of common ancestry that flowed from the aftermath of the publication of *The Origin of Species* (Darwin, 1859). Homoplasy did endure, a current definition being similarity that arises through evolutionary convergence, parallelism, or reversal.

Because we restrict our understanding of homoplasy to evolutionary parallelism or convergence *independent* of common descent and our understanding of homology to similarity by virtue of shared ancestry, we contrast homology with homoplasy and see homoplasy as the inverse of homology (Wood, 1999). In introducing the only book entirely and explicitly devoted to homoplasy (Sanderson and Hufford, 1996), David Wake summarized the relationships between these two classes as:

> Homology and homoplasy are terms that travel together; homoplasy being close to, but not quite, the inverse of homology. If homology is "the same thing" … homoplasy is the *appearance* of "sameness" that results from independent evolution (Wake, 1996: xvii).

Classes of homology

In his discussion of homology and homoplasy, and following workers such as Patterson (1982, 1988), Wake (1991), McShea (1996), and others, Meyer (1999) characterized three classes of homoplasy: convergence, parallelism, and reversals (Table 1). With respect to the developmental bases of homoplasy: different developmental pathways generate convergent characters; similar or even identical developmental mechanisms are at work in parallelism; and reversals, atavisms, and rudiments may or may not develop by similar mechanisms to those that produced the ancestral character (Table 1).

In discussing Meyer's paper (1999: 165), Wagner (2000) reinforced the concept that parallelism and convergence both provide evidence for the repeated evolution of a character: parallelism as the evolution of a character starting from the same starting point using similar developmental mechanisms; convergence involving different starting points and therefore different underlying developmental mechanisms in each lineage (Hall, 1998, 2003). A particularly nice example is lack of homology between the tests of holothurians (sea cucumbers) and the independent and secondary gain of bilateral symmetry based in a different developmental component (ectoderm)—adult bilateral symmetry having evolved three times (Kerr and Kim, 1999). It was such developmental differences that Butler and Saidel (2000) had in mind in their analysis of sameness in homology and homoplasy when they posited that the natural division might be between convergence on the one hand, and an amalgam of historical homology and homoplasy (parallelism and reversal) on the other.

Levels

In distinguishing homology from homoplasy, the level of biological organization is all important (Brooks, 1996; Wake, 1996, 1999; Lockwood and Fleagle, 1999; Meyer, 1999). When considering traits or features, homology is the persistence of similarity and homoplasy the recurrence of similarity. When considering ancestors and descendants (i.e., in a phylogenetic context), homology is the presence of a feature in the most recent common ancestor, and homoplasy is the presence of a feature because of convergent or parallel evolution (Table 2). Another levels issue is the use that is made of

Table 1
The three classes of homoplasy and their relationship to developmental pathways

Class	Definition	Development
Convergence[1]	Superficial similarity arising through independent evolution	Different developmental pathways
Parallelism	A feature present in closely related organisms but not present continuously in all the members of the lineage	Similar developmental pathways[2]
Reversals, atavisms, and rudiments	Phenotypes similar to those seen in ancestors within the lineage	Similar or different developmental pathways

[1] Meyer (1999) equated convergence with analogy.
[2] The developmental pathways may be identical in different organisms.