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ScienceDirect
Journal of Human Evolution 52 (2007) 473–479

Homoplasy and homology: Dichotomy or continuum?

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Received 30 December 2005; accepted 21 November 2006

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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0047-2484/$ - see front matter © 2007 Published by Elsevier Ltd.
doi:10.1016/j.jhevol.2006.11.010

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.

Table 2
Homology distinguished from homoplasy

At the level of traits/features	
	Homology is the persistence of similarity in evolution
	Homoplasy is the recurrence of similarity
Within a phylogenetic context	
	Homology reflects the presence of a feature in the most recent common ancestor of two species
	Homoplasy reflects: (1) the presence of a feature in two species that do not share a recent common ancestor (convergence), or (2) the presence of a feature in two species when the feature is not found in their most recent common ancestor but is present in a more distant (basal) ancestor (parallelism)

similarity/comparisons in different fields of biology. These are summarized in Table 3.

I will argue that to posit homoplasy independently of common descent is to view homoplasy in pre-Darwinian terms and in a pre-evolutionary context. Such a position also reflects what could well be an element of artificiality in the definition of homology, which defines features as homologous if shared with the *most recent common ancestor* rather than with *a common ancestor*.

I will argue that *both* homology and homoplasy reflect descent with modification, the critical differences between the two being the recency of the last common ancestor, on the one hand, and the continuous versus interrupted presence or lack of the character, on the other. The degree of modification of the feature also often differs between homologues and homoplasies, but whether developmental pathways are shared or divergent is a secondary consideration [Table 1; and see Hall (2003, 2006) for fuller developments of this thesis].

The importance of phylogeny

"Noise" often overpowers "signal" in phylogenetic analyses, reflecting the fact that homoplasy may be more common than homology in the evolutionary history of particular lineages and may appear more often in analyses that reconstruct phylogeny assuming a minimum number of changes (i.e., using parsimony). Such overwhelming convergent evolution reflects the conserved genetic and developmental mechanisms that underlie character evolution (Hall, 1998; Hall and Hallgrímsson, 2007).

Table 3
Approaches to analysis of similarity in different biological fields[1]

Field	Concept	Mode of analysis
Phylogenetics and systematics	Historical homology (synapomorphy)	Character distribution in phylogenetic trees
Phenotypic evolution	Biological homology	Mechanisms of character evolution
Comparative developmental biology	Generative homology[2]	Mechanisms of development and the evolution of development

[1] Based on Butler and Saidel (2000).
[2] See Footnote 1 for generative homology.

An important element of our understanding is that, while presence of a character may be discontinuous, the developmental basis for that character can persist uninterrupted for long periods of evolutionary time. Trace the evolutionary histories of species that share a homoplastic trait far enough back and you may well find a more distant ancestor that possessed the feature or the genetic/developmental basis for the feature, a notion that can be traced to the concept of "deep homology" or "homoiology" (Remaine, 1962; Riedl, 1978). Consequently, without a rigorous phylogeny, neither homology nor homoplasy can be recognized. Two recent anthropological studies illustrate the insights that can accrue from a careful analysis of homology and homoplasy within a phylogenetic context (see also Begun, 2007; Leigh, 2007).

Lieberman et al. (1996) set out to analyze homoplasy in early *Homo* as a way to infer evolutionary relationships between two hominid taxa, *Homo habilis* and *H. rudolfensis*. Lieberman and his colleagues first examined 48 cranial characters used in phylogenetic analyses of hominids to determine which had the greater effect on the topology of the cladogram. They then analyzed developmental and functional aspects of these characters to determine homoplasy, after which they reevaluated the cladistic analysis.

The characters analyzed in this study suggested that the two hominid species had different evolutionary affinities—*H. habilis* as a sister taxon of *H. erectus*, and *H. rudolfensis* sharing derived characters with the australopiths. The developmental/functional analysis indicated that many of the shared derived characters between *H. habilis* and *H. erectus* were homologies, not homoplasies. Working from the phylogeny informed delineation of homologies from homoplasies and highlighted the importance of defining characters critically. In another context—the diversity of morphologies of molar teeth in Cenozoic ungulates—Jernvall et al. (1996) demonstrated the utility of approaches that separate morphological from phylogenetic change.

The primary purpose in the study undertaken by Lockwood (1999) was to approach homoplasy using a data set on the postcranial skeleton in New World (platyrrhine) monkeys. The characters were mapped onto alternative trees for the family Atelidae in order to analyze patterns of character evolution. They were then used to construct hypotheses to explain the different phylogenetic trees. Multiple parallel adaptations to climbing and the associated changes in suspension were reflected in multiple homoplasies that swamp the phylogenetic information that such characters would otherwise be expected to contribute to a phylogenetic analysis. This is a situation in which a predominant behavior (climbing) is such a strong selective force that homoplasy becomes a dominant source of the shared similarity in data sets based on characters reflecting that behavioral/selective force (Lockwood, 1999; Lockwood and Fleagle, 1999; see the latter and Hall and Hallgrímsson, 2007, for further examples from anthropology).

Studies such as these reinforce homoplasy as evidence of shared ancestry, even if that shared ancestry is embedded in

the distant past. Such a realization reflects an objective situation, independent of how we choose to define homology or homoplasy with respect to the recency of the last common ancestor. Much more subjectively, and as a consequence of how we choose to define homology in relation to shared ancestry, if we did not base homology on the presence of the trait in the most recent common ancestor, distinguishing homology from homoplasy would be fraught with difficulty. If shared traits (homologues) were defined by presence of the trait in any ancestor no matter how distant, then homoplastic traits would be homologues. Meyer (1999) presented essentially similar arguments for dealing with the continuous presence of a developmental program but the discontinuous presence of the character, using the evolution of swordtails in the teleost fish *Xiphophorus*.

Common descent, developmental mechanisms, and homoplasy

Consequently, when we attempt to separate homology from homoplasy mechanistically, we are not dealing with a *dichotomy between homoplasy as parallelism/convergence and homology as common descent*. Nor are we dealing 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 modification, and, more specifically, with *common descent with varying degrees of modification*. The more phylogenetically or temporally distant the last common ancestor, the more opportunity for modification/loss and for parallelism/convergence (i.e., for homoplasy). Crawford and Wake's (1998) study of the single origin but multiple homoplastic losses of the balancer in larval urodeles is an especially nice example. The more phylogenetically recent the last common ancestor, the greater the likelihood of phenotypic similarity (i.e., for homology). However, genes are conserved and "homologous developmental processes"[1] can be used to generate homoplastic characters and vice versa. Importantly, even when the phenotypic character is lost, the genes and developmental mechanisms coding for the character can be retained. Viewed in this light, homoplasy and homology are not dichotomies but the extremes of a continuum. Given the early evolution and subsequent conservation of genetic/developmental mechanisms, homoplasy is not parallelism or convergence *rather than* common descent (although homoplasy is often described in such terms); it is parallelism or convergence reflecting shared ancestry and descent with modification. A number of issues will be explored to illustrate this position.

If we go back through the evolutionary histories of species that share a *homoplastic trait* we are likely to find a more distant ancestor that possessed the genetic or developmental bases upon which the feature is based. The repeated use of the same genes in different contexts—either within an individual ontogeny or by different (and not necessarily closely related) organisms—both confounds separation of homology from homoplasy and provides opportunities to understand how homologous and homoplastic traits arise (i.e., how features evolve and novelties arise).

Consequently, any discussion of homology and/or homoplasy in relation to developmental mechanisms are best posed—perhaps can only be posed—within the context of a sound phylogenetic analysis. Questions of mechanisms are secondary to phylogeny when assessing homology or homoplasy, although changes in morphology can be tracked without consideration of phylogeny (Jernvall et al., 1996). Homology cannot be assigned only on the basis of shared development. Many homologous features do not share homologous developmental pathways; some of the more well-described examples—regenerating lenses in amphibians, for example—are discussed by de Beer (1971), Hall (1995), Lieberman (1999), Butler and Saidel (2000), True and Haag (2001), and Leigh (2007). Similarly, homoplasy cannot be assigned only on the basis of lack of shared development, for shared developmental pathways are at the basis of parallel evolution. Therefore, we need to examine shared attributes both with regard to the depth of time since divergence of the two taxa being compared and with respect to how widely shared the character is both over time and within the group at one time. We are dealing with matters of degree, level, and continuity.

Many organisms share molecular, genetic, and cellular mechanisms. Indeed such mechanisms underpin all homologous and homoplastic features. Several classes of shared mechanisms and examples of each are noted below.

Shared cellular mechanisms

Animals share cell proliferation, cell migration, and cell-to-cell interactions as fundamental morphogenetic processes. Modifications of these fundamental processes underlie the evolution of both homologous and homoplastic characters. Atchley and Hall (1991; and see Chapter 20 in Hall, 1998) developed a model with cell condensations as the fundamental morphogenetic units and applied it to the developing dentary bone of the mammalian mandible. The dentary of all mammals consists of discrete morphological units, each of which arises from a separate condensation of cells, each of which is under independent genetic and epigenetic control (although basic genetic control is shared; Hall and Miyake, 2000), and each of which can be selected for independently of the other units. Burke's (1989, 1991) analysis of the evolution of the turtle carapace (which lies outside rather than inside the ribs) is another example. A shift occurs in the pathway of migration of skeletogenic cells to allow vertebrae and ribs to cooperate

[1] There is no generally accepted terminology to distinguish similar from divergent developmental processes involved in the production of homologous characters. Striedter and Northcutt (1991) used homologous and nonhomologous developmental precursors and processes. In order to avoid confusion with homology of structure, Hall (1992, 1998) used equivalent and nonequivalent developmental process. Butler and Saidel (2000) tied similar or divergent development directly to homology and homoplasy, respectively, when they advocated the term "syngeny" for generative homology, in which the same developmental processes are used, and "allogeny" for generative homoplasy, in which different developmental processes are used. My conclusions diverge from theirs.

with the dermal skeleton to produce a novel character—the turtle shell—that has few if any homologues among vertebrates despite sharing developmental processes with developing ribs, limb skeleton, and other elements (Burke, 1989, 1991; Gilbert et al., 2001; for further elaboration and additional examples, see Hall, 1998, 2003; for an analysis of similarity, parsimony, and homology in relation to the turtle shell, see Lee, 1998).

Shared cellular processes

Animals share basic mechanisms of cell lineage, cell differentiation, and cell death, patterning, and differential growth. Sommer's (1999) analysis of transformation in cell lineages for vulva development in nematodes illustrates how independent evolution of the same cell transformation in different species constitutes a developmental constraint that results in homoplasies. Differential growth as the mechanism responsible for generating the patterning of the digits in urodele limb buds contrasts with cell death, which is the mechanism underlying digit morphogenesis in all other tetrapods. This dramatic difference in morphogenetic mechanism has been used to argue that urodele digits are not homologues of the digits in other tetrapods (Holmgren, 1933; Hinchliffe, 1994).

Shared genes and pathways

Animals share basic regulatory genes that can be traced to distant ancestors and/or be used in animals that do not share a recent common ancestor. Thus, homoplasy could involve the same (homologous) genes as those used in far distant groups (Hall, 1994, 1998, 2003; Dickinson, 1995; Abouheif et al., 1997; Meyer, 1999).

A paradigmatic example that has emerged in the last few years is *Pax-6*, a gene that initiates the development of light sensitive cells, including the eyes, in many animal phyla. Ectopic expression of *Pax-6* in *Drosophila* imaginal discs destined to form wings or legs, initiates eye formation in the wings and legs that develop from those discs (Halder et al., 1995). *Pax-6* has been sufficiently conserved over such very long periods of evolutionary history that *Pax-6* from *Drosophila* will initiate eye development in *Xenopus*, even though fruit flies are evolutionarily very distant from frogs (Altmann et al., 1997). *Pax-6* is homologous across the animal phyla, but the eyes initiated by *Pax-6* in flies and frogs are homoplasies. It has been argued that only if *Pax-6* functioned to initiate eye development in a common ancestor of *Drosophila* and the vertebrates would their eyes be considered homologous (Dickinson, 1995). However, even this would not render the eyes homologous because the homoplasy of frog and fly eyes rests on much more than this single gene. The arguments raised (in various forms) by Spemann (1915), de Beer (1971), Hall (1995, 1998, 2003), Abouheif (1997), Abouheif et al. (1997), Meyer (1999), Laubichler (2000), and others concerning homologous genes initiating nonhomologous structures make a strong case for homoplasy reflecting shared, deep ancestry and retention of gene-signaling function.

Latent homology

Latent homology provides a further example of homoplastic structures arising from developmental bases used earlier in evolution and may underpin the concepts of pre-adaptation or exaptation (Stone and Hall, 2004; Hall and Hallgrímsson, 2007). The term goes back at least to Osborn (1902), who, in seeking to separate homoplasy from convergence, proposed treating Lankester's homoplasy as latent or potential homology, a change with which Lankester did not agree (Osborn, 1907).

Latent homology is the situation in which the developmental basis for a structure seen in a descendant exists in the developmental program that produced a different structure in the ancestor. Three examples (discussed in further detail in Hall, 1998), are:

- Early agnathan vertebrates lacked jaws (by definition) but possessed in their visceral arches and in the visceral arch skeleton the developmental precursors of jaws. The anterior visceral arch from which jaws later arose is a latent homologue of the jaws.
- Reptiles lack the middle ear ossicles found in all mammals, but they had the developmental precursors of such ossicles in the cartilages and bones of their lower jaws, the transformation of which created the middle ear ossicles during the evolution of mammals from therapsids (''mammal-like reptiles''). The lower jaw bones of reptiles are latent homologues of mammalian middle ear ossicles.
- Anterior paired appendages used for locomotion in ancestral arthropod lineages were modified into mouth parts with the evolution of the crustaceans. Ancestral arthropod appendages are latent homologues of crustacean mouth parts.

In each of these examples, the structure in the ancestor is *homoplastic* with respect to the newly evolved structure but *homologous* at the level of shared developmental basis, illustrating how homoplasy and homology represent ends of a continuum rather than a dichotomy of states. Wake summarized the significance of latent homology for homoplasy:

> Homoplasy is an alternative perspective on homology, and when we can identify a phenomenon as latent homology we begin to approach an understanding of how homoplasy relates to homology on the one hand and to the production of diversity on the other (Wake, 1999: 45).

Gene duplication/co-option

Duplication or co-option of regulatory genes can result in the formation of homoplastic structures. Examples include the fundamental similarity in the genetic basis for the development of fore- and hind limbs in vertebrates (although fore- and hind limbs within an individual are not homologues; Hall, 1998, 2007) and the surprisingly similar genetic basis underlying

segmentation in annelids and arthropods, on the one hand, and chordates, on the other, with segmentation having evolved independently in these two major groups (Arthur et al., 1999).

Conclusions

I have presented three classes of homoplasy with three developmental bases:

- convergence, which is independent evolution based on different developmental pathways;
- parallelism, which is the discontinuous presence of a character because of reuse of similar developmental mechanisms;
- reversals, atavisms, and rudiments, which arise by the use of similar or divergent developmental mechanisms.

What are the consequences for homoplasy of shared or derived genetic and developmental pathways? Structures may be lost but their developmental basis retained, providing the potential for homoplasy. Examples include atavisms, such as (1) the development of limb or tooth rudiments in limbless or toothless vertebrates in which the developmental basis for making limb buds or tooth rudiments has been retained (Hall, 1984); (2) the reappearance of the second molar tooth in the extant lynx, *Felis lynx*, when this tooth has not formed in members of the Felidae since the Miocene (Kurtén, 1963); and (3) the appearance of neomorphic skull bones in salamanders (Wake, 1991, 1999).

In addition, there is the potential for variation in present members of a population, as seen in the tail ''swords'' of male fishes of the genus *Xiphophorus* (Meyer, 1999), or in the variable patterns of fusion of carpal and tarsal bones in amphibians (Hanken, 1983; Hanken and Dinsmore, 1986). Indeed, variation in carpal and tarsal fusion patterns in one population of the salamander *Taricha granulosa* spans the range of patterns found throughout all urodeles, including patterns in ancestral species and in species more derived than *T. granulosa* (Shubin et al., 1995). This is a wonderful example of latent developmental potential available to be expressed through the evolution of homologous or homoplastic features. Given latent homology, assumptions such as parsimony in phylogenetic reconstruction are on shaky ground.

Finally, the same genes can be used to initiate the development of homoplastic and homologous structures, with such structures often appearing as novelties. Structures may be lost but the genetic/developmental potential retained. Such retained potential may be utilized later in evolution, either in related lineages (tarsal arrangements in salamanders) or in divergent and more distantly related lineages (*Pax-6* in sensory organs across the animal kingdom).

It is not surprising, therefore, that similar features persist when a feature is present in the nearest common ancestor (homology). It is also not surprising, although some will find it so, that different environments or selective pressures can trigger the reappearance of similar features (either using the same or different developmental pathways) in organisms that do not share a recent common ancestor (homoplasy).

Acknowledgements

Although they will not all agree with the thrust of this paper, I thank Jukka Jernvall, Axel Meyer, David Wake, and an anonymous reviewer for incisive comments on the manuscript. Financial support was provided by the Natural Sciences and Engineering Research Council of Canada (NSERC) Grant #A5056, and by The Killam Trusts of the Canada Council for the Arts and of Dalhousie University.

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