

## Introduction: What This Book Aims to Do and What It Is Not

Homology, the correspondence of characters from different species or even within the same organism, is a fundamental concept in evolutionary biology and biology in general (Wake 1999). It is broadly recognized that homology is explained by derivation from a common ancestor that had the same character or trait. This explanation applies at least to characters from different species. Accordingly, this concept has applications in many fields of biology by referring to morphological characters, behaviors (Lorenz 1981; Prum 1990; Griffiths 1997; Scholes-III 2008), proteins and genes, as well as to gene regulatory networks (Abouheif 1999) and developmental mechanisms and processes (Bolker and Raff 1996; Gilbert and Bolker 2001). Each of these fields has its own conceptual and technical challenges. However, beyond the most general statement that homology is a hypothesis of descent from a common ancestor, little of substance can be said regarding all of these notions of homology. Hence, it would not be particularly useful to write a book that pertains to all these forms of homology. The issues are far too heterogeneous to allow a synthetic treatment, at least at this point in history. Consequently, this book is not meant to cover homology in all its breadth. Rather, it focuses on one class of homology relationships: that between morphological characters. I made this choice for the following reasons.

Not all of the various notions of homology face the same conceptual and biological challenges. For example, the notion of gene homology may, at times, be technically challenging to demonstrate; yet at the conceptual level, it is relatively straightforward. DNA is directly inherited by cells, by individuals, and by different generations. DNA is directly copied in that the copying process itself duplicates the relevant information-carrying structure<sup>1</sup> (i.e., the nucleotide sequence). There is even material overlap between the parental DNA and daughter DNA strands; that is, in the “semi-conservative replication” of DNA, one strand of the double helix of daughter DNA is physically one of the strands of parental DNA.

Ironically, one of the most difficult classes of homology relationships to explain is the one from which the homology concept originated: the homology of morphological characters (Owen 1848). There are two reasons why

<sup>1</sup> An exception are those species in which genes do not contain all of the information necessary for mRNA (i.e., species in which extensive RNA editing occurs, as in some ciliates).

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the homology of morphological characters is harder to understand than that of genes. First is the obvious fact that morphological characters are not passed on from generation to generation by direct copying. In each generation, all morphological characters need to develop *de novo* from a fertilized or unfertilized egg cell (Wagner 1989). An obvious way forward would be to say that what is inherited are the genes necessary to engender the development of the character (Van Valen 1982). In other words, a morphological character is transmitted indirectly through the transmission of the genes that control the development of the character. This is certainly true, at least in the short term, that is, over several generations and likely within the lifetime of a single species. Over longer periods of evolutionary history, however, the correspondence between genes and character identity decreases.

There is mounting evidence that homologous characters from distantly related organisms, like grasshoppers and fruit flies, often use quite different genes for the development of clearly homologous characters, like insect body segments (see chapter 3). Hence, the identity of morphological characters cannot be explained by the *identity* of the set of genes that directs their development (Spemann 1915; DeBeer 1971; Roth 1984; Roth 1988; Wagner and Misof 1993; Hall 1994; Wagner 1994; Wray and Abouheif 1998; Hall 2003).

Because of these heterogeneous problems that are attached to the various uses of the homology concept, this book does not aim to cover all notions of homology. There will be no discussion of molecular homology, nor will there be a discussion on the homology of behavioral patterns or of physiological and developmental functions *per se*. Rather, the goal of this book is quite specific—namely, to propose a solution to the homology problem for morphological characters as sketched out in the previous paragraph. While homology of morphological characters can be viewed as being quite “retro,” going back to the comparative anatomy of the eighteenth and nineteenth centuries, the contemporary context of these problems is all but retro. Homology of morphological characters became a major theme in evolutionary developmental biology during the last two decades, mostly due to progress made in evolutionary developmental biology (see references cited above).

The developmental genetic revolution, which began with the discovery of the homeobox genes, has deepened our understanding of how the development of morphological characters is controlled by genes. It has also deepened our understanding of how changes in the expression and activity of developmental genes underlie the evolution of developmental pathways and, thus, the evolution of morphological structures (Carroll, Grenier et al. 2001; Wilkins 2002). Given that we can now understand the evolution of morphological characters as a consequence of the modification of gene regulatory networks, it is time to revisit character identity and homology of morphological characters.

This book, although ostensibly about homology, is really a book on developmental evolutionary biology. The claim can be made that a mechanistic understanding of homology can become a unifying theme for evolutionary developmental biology, as well as any other branches of science that are concerned with the structure and development of organisms. I will make the argument that one of the main benefits of a deeper understanding of homology is that it enables an empirical research program on the major transitions in evolution, in particular the origin of evolutionary novelties. I argue that the origin of novel characters and novel body plans is one of the most important but least researched questions in evolutionary biology.

Novelty and major transitions underlie the broad patterns of biological diversity by explaining the differences between major groups of animals, plants, fungi, and the vast array of protozoans and microbes. Yet very limited progress has been made in this area compared to the rich knowledge we have acquired on speciation, behavioral evolution, and adaptation. However, during the last ten to twenty years, the situation has changed, and this book aims to synthesize this new knowledge into an account of the evolution of character identity and character origination.

The argument that understanding homology is essential for making progress in understanding evolutionary novelties is based on an analogy. Ideas regarding the nature of species are essential for setting the research agenda on the mechanisms of species origination. Whatever one may think of the biological species concept of Ernst Mayr and his contemporaries (Mayr 1942), it remains a historical fact that it enabled a rich, productive study of speciation. By conceptualizing species as collections of interbreeding populations that are reproductively isolated from other populations, it is clear that the objective of a research program on the origin of species has to be the question: how do barriers to sexual reproduction and, thus, to gene flow arise? Prior to that it was not clear what species are and, thus, it was not clear how they originated, or even what the question was. This was a failure of conceptual clarity that prevented progress in empirical research. Similarly, without an understanding of what characters are, we cannot determine how they originate.

Here I will argue that the key to understanding the nature of character identity is to ask what individuates body parts both developmentally and genetically. I will propose that the key is the existence of gene regulatory networks that *enable the expression of different developmental programs* in different parts of the body,<sup>2</sup> so-called Character Identity Networks (Wagner 2007). It turns out that these networks are evolutionarily more conserved

<sup>2</sup>Note that here I am talking about gene regulatory networks that enable differential gene expression, and not about the totality of the gene regulatory network that underlies a particular character. This helps to resolve the problem of conserved and variable parts of the development of homologous characters (see chapter 3).

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than other parts of the developmental program, and are often rigidly associated with the identity of the character that they enable. From this perspective, the evolutionary origin of characters and body plans is the origin of those gene regulatory networks that underlie character identity.

At its core, this is the argument made in the remainder of this book. It will be shown that this move requires a number of conceptual adjustments, including recognizing the difference between character identity and character states (chapter 2). In addition, because certain conceptualizations of homology, as for example those made in the cladistic tradition of taxonomy, are incompatible with this program, certain adjustments in the metaphysical assumptions underlying evolutionary biology will have to be made (chapter 7). The complexity of this undertaking necessitated a book format, as this task could not have been achieved even in a long article. It is my hope that this book comes close to achieving this goal.

For really impatient readers, a one-page summary of the core conclusions of this book is provided in chapter 13 in the section entitled, “What Are the Core Claims of This Model of Homology?”