HOMOLOGY

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Homology is a specific explanation of similarity of form seen in the biological world. Similarities can often be explained by common descent; features are considered homologous if they are shown to be inherited from a common ancestor. For example, although the arms of four-limbed vertebrates externally appear quite different, all have the same basic underlying skeletal and muscular pattern. Such shared patterns are best explained by the inference that they were inherited from a common ancestor that also had this pattern. Proposed homologies are evaluated using comparative anatomy, genetics, development, and behavior.

WELLS RIDES THE HOMOLOGY MERRY-GO-ROUND...

Wells claims that homology is used in a circular fashion by biologists because textbooks define homology as similarity inherited from a common ancestor, and then state that homology is evidence for common ancestry. Wells is correct: this simplified reading of homology is indeed circular. But Wells oversimplifies a complex system into absurdity instead of trying to explain it properly. Wells, like a few biologists and many textbooks, makes the classic error of confusing the definition of homology with the diagnosis of a homologous structure, the biological basis of homology with a procedure for discovering homology. In his discussion, he confuses not only the nature of the concept but also its history; the result is a discussion that would confuse anyone. What is truly important here is not whether textbooks describe homology circularly, but whether homology is used circularly in biology. When homology is properly understood and applied, it is not circular at all.

...BACK TO THE FUTURE

Before 1859, the year Darwin published the *Origin of Species*, homology was defined as similarity of structure and position, and distinguished (although inconsistently) from “analogy,” which was defined as similarity of function but not necessarily of structure and position. An example of homology and analogy are the wings of birds and bats. The arms of birds and bats would be considered homologs because they have the same structure and position in both animals. Their wings, however, are analogs. Both wings have the same function (flight), yet the bird’s wing is made of feathers, and the bat’s is made of skin. They are different structures.

The pre-Darwinian basis for similarity was the idea of an “archetype.” The archetype, however, was never clearly defined. The idea belongs to a morphological theory that came from the German transcendentalist philosophers of the late 1700s and early 1800s. It was largely out of fashion by the 1840s, but Richard Owen, who codified this distinction, was dedicated to a philosophy of transcendental causes, as many historians of science have noted (e.g. Russell, 1916; Desmond, 1982; Rupke, 1993; Padian, 1995a, 1997).

Yet the pattern of the biological world more resembles a genealogy than a gallery of cookie-cutter “archetypes.” Darwin accounted for the similarities in structure and position among very different animals as being the result of natural selection working on shared ancestral patterns. The concept of homology shifted from reflecting a vague “archetype” to reflecting descent with modification.

Today, biologists still diagnose homologous structures by first searching for structures of similar form and position, just as pre-Darwinian biologists did. (They also search for genetic, histological, developmental, and behavioral similarities.) However, in our post-Darwin period, biologists *define* a homologous structure as an anatomical, developmental, behavioral, or genetic feature shared between two different organisms because they inherited it from a common ancestor. Because not all features that are similar in two organisms are necessarily inherited from a common ancestor, and not all features inherited from a common ancestor are similar, it is necessary to *test* structures before they can be declared homologous. To answer the question, "could this feature in these groups be inherited from a common ancestor?" scientists compare the feature across many groups, looking for patterns of form, function, development, biochemistry, and presence and absence. Many features are tested simultaneously against genealogy through a process that Kluge (1997; see also Kluge, 1998, 1999 for discussions of independent homology tests) termed testing "multiple ad hoc hypotheses of homology."

If, considering all the available evidence, the distribution of characteristics across many different groups resembles a genealogical pattern, it is very likely that the feature reflects common ancestry. Future tests based on more features and more groups could change those assessments, however — which is normal in the building of scientific understanding. Nevertheless, when a very large amount of information from several different areas (anatomy, biochemistry, genetics, etc.) indicates that a set of organisms is genealogically related, then scientists feel confident in declaring the features that they share are homologous. Finally, while judgments of homology are in principle revisable, there are many cases in which there is no realistic expectation that they will be overturned.

So Wells is wrong when he says that homology assumes common ancestry. Whether a feature reflects common ancestry of two or more animal groups is *tested* against the *pattern* it makes with these as well as other groups. Sometimes, though not always, the pattern reflects a genealogical relationship among the organisms — at which point the inference of common ancestry is made. Today, the testing process is carried out by a method called "phylogenetic systematics" or "cladistics," which can be done without assuming an evolutionary relationship among the groups — but descent with modification is the best explanation for the patterns the comparisons of features it reveals.

Evolution and homology are closely related concepts but they are not circular: homology of a structure is *diagnosed* and *tested* by outside elements: structure, position, etc., and whether or not the pattern of distribution of the trait is genealogical. If the pattern of relationships looks like a genealogy, it would be perverse to deny that the trait reflects common ancestry or that an evolutionary relationship exists between the groups. Similarly, the *closeness* of the relationship between two groups of organisms is determined by the extent of homologous features; the more homologous features two organisms share, the more recent their common ancestor. Contrary to Wells's contention, neither the definition nor the application of homology to biology is circular.

As mentioned, new evidence from various fields of biology has expanded our understanding of homology beyond just anatomical structures. Anatomical homologies, behavioral homologies, developmental homologies, and genetic homologies can be independently diagnosed and tested.

Behavioral homology recognizes features of animal behavior that can be traced to common ancestry. For example, consider the nesting practices of birds and crocodilians. Both of these groups share the behaviors of nest-building, parental care of young, and "singing" to defend territory and attract mates. Most people know birds do these things, but fewer know that their cousins the alligators and crocodiles do these things as well. They inherited these behaviors from a shared ancestor. Because of homology, we infer these behaviors for their extinct ancestors as well; thus it came as no surprise when fossils of many non-avian dinosaurs were found nesting with their young (Horner and Makela, 1979; Horner, 1982; Clark et al., 1999).

Developmental homologies are features in the developmental programs of organisms. An example of this is the "pharyngeal pouches" that nearly all vertebrates acquire to some degree during their development, but which become very different structures in the adults. For example, the embryological pharyngeal pouches of jawless chordates (e.g., *Amphioxus*, hagfishes, and lampreys) develop into pharyngeal arches and slits, which support the gill structure and allow water to exit the pharynx after passing over the gills. In jawed vertebrates, such as sharks and fish, the pharyngeal pouches develop into gill supports and portions of the jaw skeleton. In land vertebrates (tetrapods), these arches and pouches develop into jaw skeleton and musculature, but other pouches/arches, which in gill bearing vertebrates developed into gill structure, now develop into ear bones and cavities, and thyroid and tracheal cartilages (Gilbert, 2000). The evolution of the different adult pharyngeal morphologies of vertebrates are the results of alterations of these embryonic structures and their components through the developmental program (Graham, 2001).

Today we also recognize genetic homologies. There are similar genes that control the development of non-homologous features. For example, there is a gene, named "*Pax6*," possessed by fruit flies, mice, and many other organisms, which influences the development of the eye. Biologists hypothesize that the gene is inherited from a common ancestor not only because of its biochemical similarity but also because of its distribution in numerous taxa. However, the actual eyes that the gene forms are not a result of common ancestry — their shared ancestor most likely lacked eyes, although it may have had light-sensing ability. The eyes of flies, mice, and many other creatures are of different structure and position and are not historically continuous, yet the *Pax6* gene is historically continuous and responsible for them all. This homologous gene functions as a "switch" that triggers the development of light-sensing organs (Gilbert, 2000), but the "downstream" genes that they trigger are no longer the same: they govern different developmental programs and thus build structurally different eyes in flies, mice, and other organisms. The relatively new field of evolutionary developmental biology (evo-devo for short) deals with these processes. The discoveries made in just the last 10 years in this field have greatly increased our understanding of homology, and have made the picture more complex. Wells nearly ignores this important new field in his discussion, a surprising omission for one whose background includes a degree in biology.

HOMOLOGY, EVOLUTION, AND THE NATURE OF SCIENCE

Some formulations of the concept of homology appear to be circular, but as discussed above, because there is an external referent (the *pattern* that characteristics take across groups) that serves as an independent test, the concept, properly defined and understood, is not. Wells's claim that homology is circular reveals a mistaken idea of how science works. In science, ideas frequently are formulated by moving back and forth between data and theory, and scientists regularly distinguish between the definition of a concept and the evidence used to diagnose and test it.

Homology is in fact no more circular than the methods used in geology to determine paleogeography and plate tectonics. For example, in the 1920s, Alfred Wegener used the shape of the continents, the correlation of rock strata, the correlation of fossil organisms, and the position of glacial striations as evidence for his proposal that the continents were once joined in one supercontinent and have subsequently "drifted" to their current locations. Today, geologists can estimate where a certain section of a continent used to be by looking at polar wander, paleomagnetism, glacial striations, correlation of strata and fossils, and shape. Is this any more circular than the reasoning for homology? No. Evidence was used to infer that continents had moved, and then the concept of plate tectonics was applied to *different* data to determine the positions of continents at different times. The analogy to plate tectonics is also relevant to Wells's implication (Wells, 2000:77) that we don't fully understand the mechanisms of homology: the mechanism of sea floor spreading may not yet be fully understood, but the continents still move.

WHAT THE TEXTBOOKS SAY

The presentations of homology in the textbooks reviewed by Wells differ only in the lengths of their discussions. Overall, textbooks give homology (usually including discussions of analogy and vestigial features) 2–10 paragraphs (Figure 7). Because the shorter introductory textbooks have little space to devote to the complexities of how homology is defined, diagnosed, and applied, their explanations verge on the circular. The longer upper-level textbooks make a clearer distinction between the explanation for homology (common ancestry) and using sets of homologies to reconstruct relationships (Figure 7). All textbooks include diagrams of the forelimbs of various vertebrates, and all but one color-code homologous elements for easy identification. Guttman includes a second figure showing homologous bones in a number of tetrapods and one fish skull, clearly illustrating how skulls have been reshaped. Futuyma, Guttman, and Campbell, et al. include the best discussions and illustrations of homology, but nevertheless earn a D from Wells.

Most textbooks include discussions of analogy and vestigial structures along with discussions of homology. Analogous features are features with similar functions (but not necessarily similar structures) that are not inherited from a common ancestor but evolved convergently, whereas vestigial features are remnant structures that have been retained from previous forms. Wells notably leaves out any mention of analogous features or vestigial structures from his evaluation (such as the limb girdles of snakes or the limb girdles of whales cited by most textbooks).

WELLS'S TEXTBOOK EVALUATION

According to Wells, textbooks should explain that homologies are similarities of structure and function due not to common ancestry but to a common "archetype" or basic plan on which all forms were based (Wells is remarkably cagey as to what he means by "archetype"). When Wells proposes that textbooks revert to a pre-Darwinian view of homology, he doesn't explain what that would mean for biology or biology teaching. He doesn't explain that it would replace a testable model (descent) with a non-existent, untestable, transcendentalist construct. Wells is vague because he merely wants to advance his position and the archetype is consistent with some notion of special creation, as

Book	Homology			
	#pages	#words	separates homology from phylogenetic reconstruction	Wells's Grade
Schraer, W. D. and H. J. Stolze. 1999. Biology: The Study of Life, seventh edition. Prentice-Hall, Upper Saddle River, NJ. 944p.	1	309	No	D
Johnson, G. B. 1998. Biology: Visualizing Life. Holt, Rinehart & Winston, Orlando. 895p.	1	110	No	F
Biggs, A., C. Kapinka, and L. Lundgren. 1998. Dynamics of life. Glencoe/McGraw Hill, Westerville, OH. 1119p.	1	298	Yes	D
Miller, K. R. and J. Levine. 2000. Biology, fifth edition. Prentice-Hall Upper Saddle River, NJ. 1114p.	1	116	No	D
Starr, C. and R. Taggart. 1998. Biology: The Unity and Diversity of Life, eighth edition. Wadsworth Publishing Company, Belmont CA. 920p.	1/4 (1)	100 (320)	No	D
Guttman, B. S. 1999. Biology. WCB/McGraw-Hill, Boston. 1175p.	1	380	No	D
Mader, S. 1998. Biology, sixth edition. WCB/McGraw-Hill, Boston. 944p.	1/2 (1/3) +1/3	118 (241) +280	Yes, but not strongly	F
Raven, P. H. and G. B. Johnson. 1999. Biology, fifth edition. WCB/McGraw-Hill Boston. 1284p.	1/4 (1/2)	127 (207)	No	F
Cambpell, N. A., J. B. Reese, and M. G. Mitchell. 1999. Biology,fifth edition. Benjamin Cummings, Menlo Park, CA. 1175p.	3/4 (1/4) +1	193 (362) +348	Yes	D
Futuyma, D. 1998. Evolutionary Biology. Sinauer Associates, Sunderland, MA. 761p.	2	>400	Yes	D

Figure 7. *Examination of grades applied by Wells for Icon #3. Parentheticals refer to additional coverage. Plus (+) numbers reflect secondary treatments of homology and convergence in phylogenetic recontstruction sections of the text.*

favored by proponents of "intelligent design" creationism and their allies.

Wells's grades (he gives only Ds and Fs) appear to correlate with the length of the textbook's coverage (Figure 7). For example, all books given Ds devote well over 200 words to the discussion of homology, whereas the three books given an F devote fewer than 200 words. This is because the difference between a D and an F for Wells is whether the book defines homology "circularly." Therefore, the ability to treat homology "well" (meaning a D) depends largely on how much space is devoted to the discussion of it. Wells does, however, allow the book to have a picture. In order to receive a B or better, textbooks must define homology as similarity of structure and position and state that homology is based on the concept of an "archetype." Further, they should state that an "archetype" could mean many things, not just common ancestry. He also wants textbooks to state — inaccurately — that mechanisms such as genetics and developmental programs do not account for homology. Finally, he wants textbooks to state that the concept of homology is "controversial." This scheme is rigged for failure because contemporary biology does not consider homology to be either controversial or based on archetypes. There is certainly no reason to accept these grading criteria.

WHY WE SHOULD STILL TEACH THAT HOMOLOGY IS A RESULT OF COMMON ANCESTRY

As our current knowledge of biology suggests, there is no reason to doubt the fact that the patterns of structures, behavior, genes, and developmental programs fit best with the hypothesis that all organisms share common ancestors. Many of the similarities among these widely divergent groups are a result of that ancestry. The questions currently being debated in biology are not whether homology is real, but rather what structures are homologous and how we may best determine homology (because our diagnostic approaches are fallible). This type of discussion of reliability of methodology is typical for science in all fields, not just biology. Descent is the basis for homology; similar genes, acting through development, convey homology between generations. Genes build structures through their interactions in the developmental program. Therefore genes, development, and similarity of structure and position are discovery procedures for homology; they help biologists to determine evolutionary relationships. This fits the patterns and processes we observe in the natural world; this is what we should teach.

HOW TEXTBOOKS COULD IMPROVE THEIR DISCUSSIONS OF HOMOLOGY

The biggest flaw in textbook descriptions of homology is that they, like Wells, tend to confuse the definition of homology with the diagnosis of homologous features. Textbooks need to state explicitly that homologies are similarities seen in the biological world that are best explained as being due to common descent. They should then explain how homologous structures are diagnosed by their similar structure and position, biochemical basis, developmental path, and so on. A more detailed and lengthened discussion would help to remove the appearance of circularity caused by oversimplified descriptions. Describing how homology is used as a tool to discover evolutionary relationships would make it a much more pedagogically useful concept for students because it would show them how evolutionary biologists use anatomical observations to discover evolutionary relationships. Finally, adding the notions of multiple layers of homology from genetics and developmental biology would better show students just how different lines of evidence converge to support homologies and phylogenies. Textbooks should not follow Wells's suggestion to say that homology is merely similarity in structure and position, nor should they state that there are "other" reasons for homologies beyond inheritance from a common ancestor. To revert to Wells's 19th-century notion of homology would leave students unprepared to participate in 21st-century science.

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