

HOMOLOGY

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HOMOLOGY is widely considered to be among the most important principles in comparative biology (Bock, 1974; Riedl, 1978). As Colin Patterson (1987, p. 18) put it, "all useful comparisons in biology depend on the relation of homology." Yet there are still significant differences in the meaning attributed to the term (and related words such as analogy and homoplasy), even among authors professing the same general outlook. Advances in phylogenetic systematics and in developmental and molecular biology have renewed interest in homology, and recently there have been several reviews that focus attention on alternative concepts. The papers of Patterson (1982, 1987, 1988), Roth (1984, 1988), and Wagner (1989a, b) are especially valuable.

Homology and evolution. The term homology is generally attributed to the British anatomist Richard Owen, who defined "homologue" in 1843 as "the same organ in different animals under every variety of form and function." Later its meaning was extended to include what he called "homotypy" (the "same" organ *within* an organism) and "general homology" (structural resemblance to an archetype) (Owen, 1848). Owen did not take credit for the concept, citing Etienne Geoffroy Saint-Hilaire, who noted its presence in even earlier German literature (see references in Sattler, 1984). Indeed, as Wagner (1989b) points out, the concept was already developed in Goethe's writing. At the very least, however, Owen provided "precision and currency" (Lankester, 1870).

The first and most fundamental shift in the meaning of homology accompanied the rise of evolutionary thought. Owen's definition was more or less retained by Charles Darwin (1859a) and his contemporaries—homology was morphological correspondence as determined primarily by relative position and connection. But the associated explanation was radically different. Metaphysical archetypes and "essential" similarity were replaced by material ancestors that could evolve. This connection having

been made, the observation of homology could then be used as evidence for evolution and phylogenetic relationship.

Although ancestry was at first viewed only as an explanation for homology, it soon was incorporated into the definition (Haas and Simpson, 1946). E. R. Lankester's paper of 1870 played an important role, as evidenced in later editions of the *Origin*. He was critical of essential similarity and instead connected homology and related terms to common ancestry. Furthermore, he suggested that homology be subdivided. For homologous similarity due to inheritance from a common ancestor, Lankester coined the term "homogeny," and for such similarity resulting from independent evolution he introduced "homoplasy." "Analogy" then referred to similarities that would not be accepted as homologous based on standard criteria. The term "homogeny" was never widely adopted, and "homology" quickly became associated with similarity that could be traced to a common ancestor. This kind of transition—from explanation to definition—is probably commonplace (see Donoghue, 1985, on "species").

In retrospect, the connection between homology and evolution created at least two difficulties that appear to be common sources of semantic confusion (Donoghue, 1985). First, two potentially dissociable elements were combined in one definition (Boyden, 1943, 1973). If there are cases (as we suppose there are) in which similar structures originate independently, or cases in which very different structures originate through evolutionary transformation, one is forced to choose which element—similarity or ancestry—is to be given primacy. Second, homology was now expected to account simultaneously for the maintenance of similarity and for the transformation of form—for both constancy and change.

Homology as similarity. One response to these difficulties was to continue to associate homology with similarity alone. This is sometimes defended on the grounds of historical precedent, but the argument has generally been ineffective, as the meaning attached to words often changes as associated theories are modified. Alternatively, equating homology with similarity has been endorsed on the grounds that similarity is independent of, and logically precedes, the inference of common ancestry. However, precedence in an inferential process hardly implies greater importance, nor does it determine what a particular term is to signify (de Queiroz and Donoghue, 1990). Indeed, it could be argued that ancestry is fundamental, because it provides an underlying rationale for choosing among possible similarity criteria.

Others have argued that evolutionary homology is nonoperational and that it is circular to define homology in terms of ancestry if it is then to be used as evidence of ancestry (e.g., Woodger, 1945; Sokal and Sneath, 1963). These arguments are countered by Ghiselin (1966), Hull (1967, 1968), and others (see Hennig, 1966, p. 94). Here it is important to rec-

ognize that when homology is defined in terms of ancestry, particular instances are recognized by using a set of similarity criteria and by testing the congruence of presumed homologous traits with other such traits (see below). In this formulation, similarity criteria are a means of helping to identify homology, and particular similarity criteria can be evaluated on the basis of how well they do. But when homology is defined in terms of similarity, one wonders how one set of similarity criteria can be justified as better than another.

Three criteria discussed by Remane (1952) are widely cited both by those who define homology in terms of similarity (e.g., Kaplan, 1984) and by advocates of evolutionary homology (e.g., Hennig, 1966): similarity in relative position, similarity in structural detail, and the presence of transitional forms, including intermediates in ontogeny. If there are reasons for defining homology in terms of Remane's criteria, these have not been clearly stated. And if the ultimate intention is to discern which structures were derived from a common ancestor, then why not apply the word homology to traits that are actually believed to be historically unique, rather than to structures that merely conform to Remane's criteria (Sanderson, 1989)?

Even if one wished to equate homology with Remane's criteria, there are obvious difficulties when some but not all of the criteria are met. Sattler (e.g., 1966, 1984; see also van der Klaauw, 1966, and Meyen, 1973) notes that structures sometimes combine the features of two or more different organs. For example, the "phylloclades" of some monocots are borne in the position of a branch but are similar to leaves in terms of development, symmetry, and internal anatomy, perhaps as a result of homeotic mutations that cause developmental processes to occur in new locations (Sattler, 1984, 1988). To accommodate such cases, Sattler proposed that a semi-quantitative index be used to reflect the "partial homology" of the structure to a leaf and to a stem, thereby circumventing the need to assert that it is either "essentially" a leaf or a stem. Partial homology is incompatible with standard evolutionary views, according to which structures are either homologous or not (e.g., Patterson, 1987).

The so-called operational view of homology developed by pheneticists (e.g., Jardine, 1967; Key, 1967; Jardine and Sibson, 1971; Sneath and Sokal, 1973) has similar consequences. According to Sokal and Sneath (1963) two characters are operationally homologous if they are "very much alike in general and in particular." This, too, opens the way for partial homology, because the extent to which structures are similar may vary continuously. It is noteworthy that operational homology has resurfaced in the literature on morphometric techniques, wherein homology is associated with points or "landmarks" on a structure, which can then be used in calculating a series of measurements (Bookstein et al., 1985).

The equation of similarity with homology, and consequently the acceptance of partial homology, is also widespread among molecular biologists (e.g., Winter et al., 1968), despite arguments against such usage (e.g., Reece et al., 1987) and at least one journal that specifically prohibits it (Patterson, 1988, in reference to *Molecular Biology and Evolution*). Here, when it is said that two polypeptides or segments of DNA are 75% homologous, it means that they can be aligned in such a way that the same amino acids or nucleotides are present at 75% of the sites. In this context, the issue is complicated by the argument that sequences which are sufficiently similar must also be homologous in the evolutionary sense, simply because the chances of independently acquiring a high percentage similarity are vanishingly small (for examples of such calculations, see Fitch, 1966; Doolittle, 1981; Dayhoff et al., 1983; Karlin et al., 1983).

Transformational homology. A more popular view is that structures are homologous if they can be traced to a particular condition that originated once in a common ancestor (Simpson, 1961; Hennig, 1966; Mayr, 1982a). This includes retention in a more or less unchanged form or transformation, directly or sequentially (and possibly radically), from an ancestral condition. Similar features that originated independently from states in different ancestors are not homologous. Such cases, whether involving reversal, convergence, or parallelism, are generally covered by the term "homoplasy" (Sanderson and Donoghue, 1989; but see below). "Analogy" also commonly means the opposite of "homology" (e.g., Haas and Simpson, 1946; Riedl, 1978), but it is restricted by some authors to cases of convergent similarity shaped by selection, or even to similar function regardless of ancestry (Owen's original definition; see Boyden, 1943).

One set of difficulties with the transformational view of homology concerns the range over which the term is to be applied. According to Riedl (1978, p. 41) the lower limit of applicability—the "homonymy limit"—is the level at which one encounters a large number of virtually indistinguishable building blocks (e.g., bone cells). At the other end of the spectrum, Riedl identifies organisms, considering it inappropriate to refer to whole organisms as homologous with one another. But these ideas are not universally accepted. Rieger and Tyler (1979) extend homology to ultrastructural features, while Patterson (1988) and Nelson (1989) would use homology in reference to organisms, and even species or "higher" taxa. There is also disagreement about whether homology should be limited to structures or extended to encompass functions and behaviors (see Hubbs, 1944; Haas and Simpson, 1946; Cracraft, 1981; Lauder, 1986, 1990).

A related difficulty concerns the distinction between homology and non-homology. Some evolutionary taxonomists (e.g., Hecht and Edwards, 1977) have promoted the view that homology excludes convergence but includes parallelism, where the latter is interpreted as independent deri-

vation from a condition in a single common ancestor (see also Vavilov, 1922; Mayr, 1974). Although this view is rejected by many authors (e.g., Simpson, 1961; Hennig, 1966; Holmes, 1980), some use the term "homoiology" to refer to instances of independent derivation in closely related taxa or within "narrow kinship groups" (Hennig, 1966, p. 117). However, homoiology has also been used to mean "analogies on a homologous base" (Riedl, 1978; Patterson, 1982) and has been applied more broadly, even to the independent derivation of structures such as the "fins" of fish and whales. Clearly, parallelism and convergence grade into one another if the distinction is based solely on some estimate of the relative distance of ancestors.

Perhaps the greatest tension in the literature on evolutionary homology revolves around the role of similarity. Earlier definitions explicitly refer to structural similarity, but the tendency has been to drop such references (Patterson, 1982), on the view that transformation is logically independent of similarity. After all, two structures may be effectively identical yet derived independently, or they may be derived from the same precursor but so highly transformed that they are not at all similar. Bock (1963) made the latter argument in reference to the ear ossicles of mammals (see also Cracraft, 1967; Mayr, 1969). The counterargument (e.g., Ghiselin, 1969b; Inglis, 1970) is that even though homologous structures may be very different, "without some similarity, we should not even dream of homology" (Stevens, 1984, p. 403). In fact, similarity is evident in the conditional phrase (often implicit) that specifies what exactly is being compared. Thus Patterson (1982, p. 24) maintains, in reference to Bock's example, that the stapes in mammals is similar to the hyomandibular of sharks "as that element of the gnathostome hyoid arch which articulates with the braincase."

Taxic homology. One response to difficulties with the transformational view is to equate homology with the term "synapomorphy" (Patterson, 1982), where the latter is taken to mean a derived trait characterizing a monophyletic group. For Patterson the underlying motivation is to tie homology, which he believes "exists only in the human mind" (Patterson, 1982, p. 59; Nelson, 1970), to something that exists in the world, namely, monophyletic groups. Homology becomes "the relation through which we discover" monophyly, and the result is what Patterson called the "taxic" view of homology. Much the same view is evident in earlier cladistic literature (e.g., Eldredge and Cracraft, 1980; Rieppel, 1980; Wiley, 1981; Nelson and Platnick, 1981) and has since been adopted by other systematists (e.g., Stevens, 1984; see also Rieppel, 1988).

The taxic view squares nicely with the traditional evolutionary view if monophyly is defined in terms of common ancestry, as it is by phylogenetic systematists *sensu* Hennig (1966). And when it is appreciated that homol-

ogy includes both synapomorphy and symplesiomorphy (because the latter are synapomorphies that circumscribe more inclusive monophyletic groups), this view is also consistent with the observation that homologies are arranged in a hierarchy corresponding to the hierarchy of taxonomic groups (Bock, 1963, 1974, 1977; Riedl, 1978).

The main departure from the standard evolutionary view concerns the emphasis placed on identifying transformations. Evolutionary definitions focus on how attributes are related in the sense that one was transformed into another during the course of evolution. Under the taxic view this becomes irrelevant. Instead, it suffices to identify which characters mark monophyletic groups, regardless of exactly where these traits came from. Patterson illustrates this difference in analyzing controversies over the derivation of mammal ear ossicles: all that matters under the taxic view is whether the incus and malleus are in fact synapomorphies of mammals. Curiously, Patterson (1982, p. 36) concedes that "the transformational approach to homology may be more informative, and a lot more interesting, than the taxic approach." Indeed, the transformational approach forces us to try to connect characters to one another—to formulate bolder hypotheses.

A corollary of the taxic view is that nonmonophyletic groups are characterized only by nonhomologous features. This seems clear enough in the case of polyphyly, but Patterson means to include paraphyletic groups as well. Thus, although the scales in lizards and crocodiles are homologous, scales are not a homology of "reptiles" but of all amniotes, when the derived (transformed!) states of birds and mammals are also considered. It is even more tempting to think of homologies of paraphyletic groups in cases of secondary loss; for example, the loss of wings in some lines of insects (compare Patterson, 1982, and Hennig, 1966, p. 95). The taxic view contrasts in this regard with standard evolutionary definitions, which do not directly connect the status of groups and the status of character transformation series. The question, then, is whether there is any value in maintaining some terms to reflect the phylogenetic relationships of groups (mono-, para-, and polyphyly) and their characters (synapomorphy and symplesiomorphy), and other terms (homology) to reflect a relationship among character states, irrespective of group membership (Sanderson, 1989). Patterson's taxic view ties these together, as though there were only one legitimate concern. In contrast, Hennig (1966, pp. 95, 120) recognized related but separate concerns (see also de Queiroz, 1985, p. 294; Sober, 1988, p. 117).

Patterson's perspective is especially useful in focusing attention on tests of homology, which include *similarity* in position, structure, and development; *conjunction* (or coexistence) of presumed homologues in a single organism; and *congruence* with other presumed homologies. Of these, he

singles out congruence as the most valuable (at least for morphological data; see Patterson, 1988). The basic idea is to hypothesize that states are homologous based initially on similarity criteria and then to test this by including the character in a cladistic analysis to see whether it actually marks a monophyletic group (see also Wiley, 1975; Rieppel, 1980; Stevens, 1984). Notice that this relegates Remane's primary criteria to a role in initial evaluation and elevates congruence (one of Remane's auxiliary principles, which was meant to apply only to simple characters) to the ultimate role in establishing homology.

Patterson's analysis also allows a rather clean distinction among different forms of homoplasy. Convergences fail both the similarity and the congruence tests (although in practice such "characters" are usually rejected before cladistic analysis). Parallelisms, however, pass the similarity test but fail the congruence test. Homonymy (repeated units within an individual organism, such as hair; Riedl, 1978) or serial homology (repeated units arranged along the body axis, such as leaves on a plant) is indicated by failure of the conjunction test. Patterson (1987, 1988) pointed out that paralogous genes (Fitch, 1970) also belong in the last category, at least when organism phylogeny is being considered (e.g., the globin gene family in vertebrates).

Development and homology. The taxic view of homology elevates the ancestry component of traditional evolutionary definitions to supreme importance, while deemphasizing the retention and transformation of characters. Another response takes the opposite tack, playing down the unique origin of traits while emphasizing mechanisms responsible for character retention and transformation, especially the developmental basis of constraint. This approach, developed to some extent in G. R. de Beer's *Homology, an Unsolved Problem* (1971b), finds perhaps its fullest expression in Rupert Riedl's *Order in Living Organisms* (1978). More recently, it has been taken up by Louise Roth (1984, 1988) and, independently, by a former student of Riedl, Gunter Wagner (1989a,b). As evidenced by the titles of their papers, both wish to formulate a so-called biological concept of homology—one that encompasses homology concepts of all sorts and accounts for the underlying observations in developmental terms. In contrast to Patterson's view, the emphasis is squarely on causes, and little attention is paid to testing hypotheses of homology.

Iterative homology, including homonymy and serial homology, has been a central concern in this literature. Although this is often not admitted as true homology (e.g., Boyden, 1943; Mayr, 1982a), which is generally said to deal with comparisons among organisms or species, proponents of the biological concept insist that it be considered alongside standard homology (Moment, 1945; Ghiselin, 1976; Van Valen, 1982; Roth, 1984, 1988; Wagner, 1989a,b). As Riedl (1978, p. 38) put it, "in the last analysis we

are dealing with the same mechanism which is of the same fundamental importance . . . whether such identical individualities become separated from each other to occur in different individuals or whether they replicate within the same individual."

In her first paper on homology, Roth (1984, p. 27) explored the view that it is "based on the sharing of pathways of development which are controlled by genealogically related genes." Several conclusions follow from this. First, homology cannot be viewed as an all-or-none phenomenon (cf. "partial homology," discussed above). Instead, Roth (1984, p. 18) argues that "it is important to recognize *degrees* of homology," with the strength determined by the stage at which developmental paths diverge. She proposes, for example, that petals are more strongly homologous to leaves than sepals are. Second, she concludes that "at some level, distinguishing homology from parallelism will neither be possible or useful" (1984, p. 23), and that insisting on doing so would render the concept nonoperational because identical mutations can arise independently within interbreeding populations.

In her paper of 1988 Roth opts instead for Van Valen's (1982) definition of homology: "a correspondence between two or more characteristics of organisms that is caused by continuity of information." This, she maintains, has the virtue of being the most comprehensive, ideologically neutral, and flexible definition (although Ghiselin's [1976] definition—"parts that arise from the same source"—may be equally flexible). It also accommodates the recognition that conservatism at one level—genetic, developmental, or morphological—is not necessarily mirrored at other levels. Indeed, Roth emphasizes ways in which these levels can be dissociated, including changes in embryological source tissue, changes in inductive relationships, and what she calls "genetic piracy." The last refers to cases in which genes are "'deputized' in evolution; that is, brought in to control a previously unrelated developmental process" (Roth, 1988, p. 7).

Wagner (1989a,b) covers many of the same points in his papers, but from a somewhat different angle. For example, he emphasizes that morphological characters are not replicators, that is, that they are "not directly inherited but are built anew in each generation" (Wagner, 1989b, p. 54; see also Sattler, 1984). However, Wagner is not satisfied with Van Valen's definition of homology. As he says, "its charm as well as its weakness lies in the term 'information,' which does not imply a particular mechanism" (Wagner, 1989b, p. 60). He prefers a developmental definition, but one focused specifically on aspects of development that constrain modification: "structures from two individuals or from the same individual are homologous if they share a set of developmental constraints, caused by locally acting self-regulatory mechanisms of organ differentiation" (Wagner, 1989b, p. 62). This obviously applies to iterated structures and cases of

differentiation between the sexes (e.g., penis and clitoris), but it is much more restricted than other views. It is difficult, for example, to accommodate such things as nucleotide substitutions and color variants, and it is unclear whether it applies to behavioral traits. Furthermore, Wagner's definition says nothing of ancestry, and it is compatible with phylogenetic definitions only insofar as structures that qualify as homologous under Wagner's view are also likely to be historically unique.

Wagner's treatment is especially valuable in focusing attention on the individuation of parts. As he points out, traditional comparisons have sometimes focused on structures that are not individuated (even though they appear to be), such as tarsal elements in vertebrates (Goodwin and Trainor, 1983) or the cones of mammalian teeth (Van Valen, 1982). By way of explaining the origin and maintenance of individuality Wagner develops the idea of "epigenetic traps." These include hierarchical ontogenetic networks, with the property that some characters have greater "burden" (dependent traits or downstream effects; Riedl, 1978) and therefore are likely to be more highly constrained (see also, Wimsatt, 1986; Arthur, 1988; Donoghue, 1989). Cyclical networks, wherein traits are mutually coupled through inductive relationships, can result in even greater constraint (Wagner, 1989a).

Some developmental biologists have taken a more extreme view of homology than have the authors discussed here. For example, Goodwin (1982) believes that attention to the generative dynamics underlying morphogenesis will allow a return to "the original definition of homology": "an equivalence relation on a set of structures, partitioning the set into classes whose members share certain invariant internal relationships and are transformable one into the other while preserving the invariance" (Goodwin, 1982, p. 51). In this context, "transformation" is not to be interpreted in historical terms, but instead refers to the possibility of deriving one structure from another in a formal, atemporal sense. If not for the difference in motivation, Goodwin could easily be allied with those who hold a classical or phenetic view of homology.

The history of the word homology can be interpreted as a series of responses to challenges brought on by underlying conceptual changes. The rise of evolutionary thought forced a reconsideration of the meaning of homology and related terms. In turn, the recognition that similarity and common ancestry do not necessarily coincide resulted in an important split, some biologists preferring to maintain the connection between homology and similarity and others opting to associate homology with ancestry. Those who chose similarity faced the problem of justifying the selection of similarity criteria. This led, along several paths, to the notion of partial homology. Those who pursued ancestry faced other difficulties,

aside from the usual demands for an operational definition. The problem of identifying transformations suggested the possibility of shifting the focus to monophyly—Patterson's taxic view. In contrast, the indirect inheritance and iteration of morphological traits suggested a definition based on developmental mechanisms that account for the individuality and conservation of structures—the "biological" view of Roth and Wagner.

The homology problem focuses attention on issues of even greater generality. The choice of definitions is dictated to a large extent by how narrow or how broad one wishes to be. Patterson is satisfied to equate homology with synapomorphy, which has as one of its benefits the ability to specify critical tests. Roth apparently wants to avoid associating homology with any one theory, seeing virtue in a definition that is all-encompassing. Achieving consistency with every version of homology may yield a definition that is of little use to anyone, however. Wagner's definition, in contrast, may be overly specialized, as it excludes structures and events that are of considerable interest.

The choice of a definition is, at least in part, a means of forcing other scientists to pay closer attention to whatever one thinks is most important. It is hardly surprising, therefore, that morphologists such as Kaplan and Sattler favor definitions of homology that focus attention on position, structure, and development, for these are the aspects they find most interesting. Patterson's taxic view focuses attention on monophyly and away from identifying individual transformations, which he presumably hopes will result in more interest in cladistics. Roth and Wagner focus on retention and transformation almost to the exclusion of ancestry, hoping to stimulate more studies of the genetic and developmental mechanisms underlying constraint. For better or for worse, the choice of definitions helps determine whose agenda will attract the most attention. Fortunately, however, attention to the variety of legitimate concerns associated with the term homology is not entirely dependent on the choice of a definition.