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HOMOLOGY, FORM, AND FUNCTION

George V. Lauder

School of Biological Sciences
University of California
Irvine, CA 92717

I. INTRODUCTION

As part of our introduction to biology as undergraduates, most of us were taught the distinction between homology and analogy. Homologies are commonly presented as structures sharing common ancestry, while analogies are presented as similar structures that do not share common ancestry. Homologies may be either similar in structure (e.g., the femur of a cat and a dog) or quite different in appearance. On the other hand, the similarity among analogous characters is explained as being due to common functional or environmental demands imposed on those structures. Insect wings and bird wings are the textbook exemplar of choice. Two important issues arise from this classical explication of homology/analogy and pervade current literature discussions of these concepts.

First, analysis of the concept of homology has been overwhelmingly dominated by an emphasis on structure or form. Most definitions of homology use the term *structure*, involve only discussions of structures, and most authors restrict themselves to structural examples. Some authors have even claimed that the concept of homology applies only to structures and cannot be applied to organismal functions or other traits. More prevalent is the suggestion that without an analysis of structural underpinnings, meaningful analyses of character homology cannot take place. Under this latter view, nonstructural organismal traits such as behaviors cannot be examined exclusive of structures, hence the study of nonstructural characters is logically subservient to the analysis of structural homology. Indeed, the classical notion that function is studied for the purpose of defining analogies rather than homologies reflects the historical bias that has relegated the study of nonstructural characters to a role in identifying nonhomologous traits.

In this chapter I argue that restricting the definition of homology to structures or basing homology of nonstructural characters on an analysis of morphology is unnecessary if an explicitly phylogenetic definition of homology is used. In addition, recognition of the hierarchical nature of organismal design in which many different kinds of traits may be considered as homologues — e.g., structures, functions, behaviors, developmental pathways, and patterns of gene expression —

opens up new and exciting questions about the evolution of form and function.

Second, if the study of character function is a guide to analogy, what is the key to identifying homology? In this chapter I argue that literature on homology is pervaded by a search for the "locus" of homology in the organism: what aspect of organismal design is best for reliably identifying homologous characters? Suggestions for reliable indicators of homology include common developmental patterns, gene sequences, the structure of the nervous system, physiological patterns, and connections among structures themselves. Much of the literature on homology is devoted to arguing in favor of one of these "indicators" of homology: e.g., homologous characters can be recognized by similarity in development, connection, and/or underlying genetic structure.

I discuss below my alternative view: that the search for a locus of homology is fundamentally misguided, and that no matter how similar two organismal traits are (in development, structure, and function) they might still be nonhomologous. In contrast to the approach of recognizing homologues through an analysis of one particular class of data, I advocate a *phylogenetic approach* in which homologous traits are recognized *a posteriori* as a consequence of a global phylogenetic analysis of many characters of all kinds. A phylogenetic approach to homology gives primacy to no one class of data and allows novel questions to be asked about historical patterns of character covariation.

II. HOMOLOGY AND STRUCTURE

The notion that homologous traits of organisms are primarily structural in nature has a long pedigree in biology, founded in debates on the correspondence among parts of organisms that characterized the first half of the nineteenth century (Appel, 1987). Although discussions of archetypes, the correlation of parts within a species, and correspondences of structure across species had strong pre-Darwinian foundations (Russell, 1916; and see Chapter 1), the essential framework for analysis of the relationships among organismal traits carried over into the post-Darwinian era. Many authors, including Darwin, have recognized that traits other than structures in two or more species might be considered to share

common ancestry and thus be homologous (e.g., Ghiselin, 1976; Mayr, 1969), but a pervasive theme in the literature on homology is primacy of structural data. Since characters such as behavioral traits and physiological functions can be difficult to link to specific structures, questions have been raised as to the relevance of the concepts of homology and analogy to the analysis of function and behavior.

Table I summarizes a few of the many recent statements supporting a structurally based view of homology. Even Richard Owen's oft-quoted definition of homology as "the same *organ* in different animals under every variety of form and function" (my emphasis) carries with it an implicit structural bias: homologous attributes are organs, structural entities within the organism. In part, the focus on structure in Darwin and Owen's time may have been because information on organismal form constituted the primary data available and thus a natural focus of attention. The rise of experimental and physiological studies of organisms [of increasing interest in Berlin and France during the nineteenth century (Allen, 1975; Coleman, 1977)] occurred primarily in medical schools and had not yet begun to generate comparative data that might have raised questions about the correspondence of function across taxa. Similarly, comparative studies of behavior were not widespread, and few data were available in the last half of the nineteenth century on the distributions of behavioral characters among species. Paleontological discoveries, often a source of new taxa at the time (Desmond, 1982), provided little information on function or behavior.

The homology literature of the last 20 years has maintained the focus on structure (see Table I), at the same time as our growing ability to analyze organismal function has played an increasing role in generating functional characters in a diversity of organisms. In fact, an interesting distinction has developed in the literature between the study of structure and homology on the one hand, and the study of function and analogy on the other. This dichotomy leads to confusion in cases where it is desirable to infer function from structure in taxa in which function has not (or cannot) be studied experimentally.

Paleontologists, for example, often infer function in extinct taxa by reference to living species. Raup and Stanley, in their text on paleontology, ask us to:

Table I. *Selected Statements from the Literature Illustrating the View That the Concept of Homology Applies Only to Structural Characters or to the Structural Basis of Nonstructural Traits such as Behaviors or Functions.*

Reference	Comment on structural basis of homology
1. Atz (1970, p. 68)	"The extent to which behavior can be homologized is directly correlated with the degree to which it can be conceived or abstracted in morphological terms."
2. Wilson *et al.* (1973, p. 633)	"Homology is defined as correspondence between two structures which is due to inheritance from a common ancestor."
3. Hodos (1976, pp. 165, 161)	"The concept of behavioral homology is totally dependent on the concept of structural homology..." and "The issue is the degree to which behavior can be related to specific structural entities."
4. Riedl (1978, p. 33)	"Homologies ... are structural similarities which force us to suppose that any differences are explicable by divergence from identical origin."
5. Goodwin (1984, p. 101)	"Homology is an equivalence relation on a set of forms which share a common structural plan...."
6. Carroll (1988, p. 6)	"Homology refers to the fundamental similarity of individual structures...."
7. Wagner (1989, p. 51)	"Only morphological equivalence in terms of relative position, structure, and connections with nerves and blood vessels counts."
8. Hall (1992, p. 57)	"The author's present position is that the term homology should be limited to structures and not used for developmental processes at all ...."

consider first the case in which fossil and Recent taxa that bear sim-
ilar structures are closely related and the structures are judged to
have had a common origin. The fossil structure may then, by homol-
ogy (having the same origin), be judged to serve the same function as
does the Recent structure, (Raup and Stanley, 1971, p. 166.)

This statement reflects a common view (criticized else-
where; Lauder, 1993) that functions and structures are tightly
linked and that if two taxa share a common structure, those
structures may be inferred to have shared a common function
as well. Within this framework, homology of structures implies
homology of function.

But it is common to discover a fossil possessing a novel
structure not found in immediate relatives. How then do we
infer the function of that structure? One way is to use analo-
gous structures in Recent taxa (where function may be studied
directly) unrelated to the fossil taxon of interest (Raup and
Stanley, 1971). Thus, if two unrelated taxa (one fossil and one
recent) each possess a trait that is similar in structure and
that is analogous (that is, has evolved convergently), then in-
ference of function in the fossil taxon will depend on the
assumption that analogous structures possess analogous
functions. We are then using analogy in structure to infer
analogy in function, again assuming that structure and func-
tion tend to show concordant historical patterns, an assump-
tion that is often false (Lauder, 1993).

III. SEARCHING FOR THE LOCUS OF HOMOLOGY

The view that structure is a primary vehicle for the
recognition of homology and also the primary reference point
for the analysis of historical patterns in other types of charac-
ters (functions, behaviors, and developmental pathways) is but
one aspect of a more general issue that permeates the homol-
ogy literature. I term this issue the search for the "locus" of
information about homology: the search for (or use of) a spe-
cific class of data that contains the information necessary to
make decisions about homology by reference to characters
themselves. Note that by referring to the "locus" of homology I
do not mean a specific anatomical site within the organism,
but rather a specific class of data that is believed to contain
information best reflective of "true similarity" and thus homol-

ogy. In other words, if only we could understand more details of character structure, interconnection, development, function, or neural control (choose one), we would be able to decide if two characters are homologous.

I have previously classified such criteria for homology as *a priori* criteria (Lauder, 1986), because the goal of using a particular class of information (such as ontogenetic, structural, or neural data) is to shed light on character homology solely by a detailed analysis of the substrate for the characters themselves (that is, prior to and independent of, a phylogenetic analysis). In contrast, the phylogenetic method discussed in Section IV recognizes homologies *a posteriori*, as a result of (after) a phylogenetic analysis of many characters, not just those of initial interest.

At various times, virtually every possible class of data has been advocated as the locus in which homologous similarity among characters is revealed. Five types of data have been especially prominent in the homology literature as proposed sources of information on character homology, and these will be considered *seriatim* below.

A. Structure as the Locus of Homology

Advocates of morphology or structure as a guide to homology have suggested that the locus of homology for nonstructural characters lies in the link between these types of characters and structure. The two most commonly used nonstructural characters are functions and behaviors, and while these two classes of characters have been viewed as labile and difficult to homologize, structural features themselves have not been seen as posing problems for applying the concept of homology.

Behaviors and functions, then, might be considered homologous to the extent that we can assign an identifiable structural correlate to these behaviors and functions. The homology of nonstructural traits depends wholly on our ability to locate homologous structures. Structures themselves are often held to be homologous on the basis of an analysis of details of those structures (such as histology, the relative position of joints, tubercles on bones, or muscle attachments).

The quotations summarized in Table I encapsulate the sentiment that dominates the literature on the importance of structural data as a basis of homology. Not only is the concept of homology often restricted to morphology (or to the morphological basis of nonstructural characters), but the methods for recognizing homologies are frequently limited to the investigation of morphological data. To be sure, a number of authors have been explicit in their recognition that structures are not the only organismal traits that might be considered homologous (Baerends, 1958; Gans, 1985; Ghiselin, 1976; Greene and Burghardt, 1978; Hinde and Tinbergen, 1958; Mayr, 1969) but even in recent treatments structure is given the dominant role in analyzing homology (e.g., Wagner, 1989).

The strongest advocates of the primacy of structure in studying the homology of traits have been Atz (1970) and Hodos (1976), and much of the debate on the application of the concept of homology to behavior has centered on the role of morphology (Lauder, 1986; Wenzel, 1992). Atz (1970) argued that the lability of behavior and function make identifying such traits difficult, and that homology is thus best applied to morphology (Table I): structure alone should be the guide to comparing behavior across species. Hodos managed to divorce the concept of behavioral homology from phylogeny (and tie it to structure):

> The degree of phyletic relatedness is not the issue in behavioral homology ... the issue is the degree to which behavior can be related to specific structural entities. (Hodos, 1976, p. 161.)

The use of a morphological foundation for the study of behavioral evolution can also be found in Simpson (1958), who used a morphological criterion to maintain that one would not expect to find homologous behaviors between taxa such as arthropods and vertebrates. As these two groups possess nonhomologous skeletal systems, how could behavior be homologous:

> Divergence and lack of homological behavior between insects and vertebrates are again illustrated, for the external skeleton-internal muscle apparatus of an insect obviously had a different origin from the internal skeleton-external muscle apparatus of a vertebrate. (Simpson, 1958, p. 509.)

Today we might note as an aside that many of the genes involved in coding for muscle proteins would be considered homologous between insects and vertebrates, and that an homologous morphological substrate does in part exist. But arguments for the primacy of structural homology in the evaluation of other types of characters (behaviors and functions) are still common.

For Atz (1970) and Hodos (1976) the relationship of behavior to a morphological substrate is of such primacy that phylogenetic evidence for or against homology is subservient to the message from structural analysis. Wagner (1989) has continued this theme, separating homology from phylogeny by defining homology in terms of structure and development:

> 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, 1989, p. 62.)

This definition of homology recalls Owen's pre-Darwinian formulation, and detaches the concept of homology from phylogeny by placing the locus of homology firmly in a structural and developmental setting.

B. The Nervous System as the Locus of Homology

The nervous system has played such a dominant role in discussions of the homology of nonstructural characters such as function and behavior that I treat it as a separate class of the structural criterion for homology described above. Behavioral biologists, in particular, have commonly referred to the nervous system as a locus of homology (Lauder, 1986). For example, in discussing how one might recognize homologous behaviors, Pribaum (1958, p. 142) says that "...uncovering a behavioral process which ... is shown to depend on homologous neural structures provides a valid criterion useful in a taxonomy of behavior....," a sentiment repeated by Hodos (1976, p. 163), who stated that "Behaviors associated with brain structures that have a common genealogical history are homologous, whether or not the behaviors are of the same type or serve the same function to the animal." Baerends (1958, p. 409) argues that the pattern of motor output from the central

nervous system is critical to judgment of behavioral homology: "Our considerations lead to the conclusion that in comparative ethology it is most essential for homology that the patterns of muscle contraction should be largely identical."

There are a number of rather severe difficulties with using nervous system structure or function as the deciding criterion for behavioral homology (Lauder, 1986).

First, homologous neural structures may produce a wide variety of patterned motor output, all of which involve the same structural circuits regulated by neuromodulators (see Harris-Warrick *et al.*, 1992; Meyrand and Moulins, 1988a,b). If protraction and retraction movements of an appendage are produced by the same (homologous) structural neural circuit in two species as a result of modulation by the presence or absence of a neuropeptide, should we insist that these two behaviors are homologous?

Second, identifying structural similarities in the nervous system is difficult; for the vast majority of behaviors we have no idea of the underlying neural pathways. Even identifying the individual neurons in a similarly designed neural circuit in two species may be a challenging task, requiring information on synaptic connections, physiological activity of the neuron, and response of the neuron to modulators (Katz and Tazaki, 1992). Indeed, the whole notion of what a neural circuit is has become more vague as the flexibility of design in circuitry underlying behavior has become apparent: neural circuits are much more than just the pattern of structural interconnections among nerve cells (Getting, 1988; Harris-Warrick, 1988). Multiple circuit designs may generate similar behaviors, and components of circuits may come and go (phylogenetically, ontogenetically, and as a result of changes in external conditions such as light and temperature) while the behavior produced remains similar.

Third, the concept of a neural criterion for behavioral homology depends on a tight link between historical changes in the structure of the nervous system and in behavior. There is now good evidence that such a linkage does not necessarily exist (Kavanau, 1990; Lauder, 1986, 1991; Paul, 1991; Striedter and Northcutt, 1991) and that there may be considerable divergence in circuit morphology, motor output, and behavior within a clade. If there is no necessary link between changes in the nervous system, physiology, and behavior, then

what basis is there for assigning the locus of behavioral homology to the nervous system?

C. Developmental Patterns as the Locus of Homology

Ontogeny has long held a fascination for biologists because it is one of the few ways we have to observe structural transformation directly. Perhaps the accessibility of structural change has contributed in part to the view that a proposed homology between two structures is best examined by studying development: in order for two structures to be homologous, they must share developmental patterns or be derived from a common embryological tissue source. By a study of ontogeny we can compare the transformation of two structures; if the transformational patterns are similar we may conclude that the structures are homologous.

Roth (1984), for example, stated unequivocally her view that developmental pathways are the means by which homologous characters should be recognized:

> ... the basis of homology in the broad sense is the sharing of pathways of development,....A *necessary* component of homology is *the sharing of a common developmental pathway.* (Roth, 1984, pp 13 and 17, emphasis Roth's.

Katz and Tazaki (1992, p. 227) state that "There are a number of ways of demonstrating homology. The most rigorous is to show that two structures have the same embryological origin ...." A similar view on the importance of development has been argued by, among others, Riedl (1978) and Wagner (1989, p. 62), who suggested that homologues are "developmentally individuated parts of the phenotype."

In 1988, Roth reversed herself and concluded that development may not be such a good guide to homology, using examples from de Beer (1971) to argue that "homologues....do not always develop in a similar fashion" (Roth, 1988, p. 5), and that both the embryological processes and precursors of characters that should be considered homologous may differ. A number of authors have discussed the problems associated with a developmental definition of homology (e.g., Rieppel, 1988), and examples of such difficulties are provided in Hall (1992) and Raff et al. (1990).

If adult phenotypic features in a group of related species (that to all appearances possess structure and patterns of connection similar to surrounding structural elements) differ in their pattern of development, what utility is there in assigning priority to developmental data as the locus of homological information? Similar phenotypes may result from a diversity of ontogenetic processes. Perhaps the specifics of developmental patterns used to generate an adult structure are not necessarily closely linked to the form, function, or history of the structure itself. In such cases, we would expect the history of developmental pathways in a clade to be different from that of the resulting phenotypic trait.

D. *Genetic Data as the Locus of Homology*

The notion that homology is a relationship written in the genes is a tempting one, given that the genetic material does contain in coded form at least part of the information needed to generate phenotypic traits. As a result, genetic data (usually gene sequences) have been advocated as a locus of phenotypic homology. Hickman *et al.* (1988, p. 114) state that "The best criterion of homology would be the identification of homologous genes." Roth (1984, p. 18) states that "...I would reject a suggestion of homology if structures are created by unrelated sets of genes." Thus, if we wished to determine if two structures are homologous we could locate the genes that code for proteins and regulatory factors in the development of those structures and examine the gene sequences.

Aside from the obvious practical difficulties in applying this research program for analyzing proposed homologies, we face the difficulty of determining if the genes themselves are homologous, using any of the above *a priori* criteria, even assuming that we can identify the correct genes. At this stage, most of the previously mentioned criteria break down; we cannot study the ontogeny of a base pair, or analyze its structure.

There are additional difficulties with ascribing the locus of homological relationship to genes: similarity in genetic sequence is no guarantee of similarity in phenotypic traits, due to the intervening complexities of epigenetic interactions and regulatory genes and pathways. In addition, quantitative genetic analyses in combination with selection experiments

demonstrate that similar phenotypic end–products of selection for a specific trait (such as tail length) may be produced by different evolutionary pathways, resulting in different patterns of genetic correlation among traits in replicate lines (Rutledge et al., 1974). Lenski (1988) showed that resistance to T4 virus infection in replicate lines of *Escherichia coli* may be achieved via different genetic changes: the similar phenotype of T4 resistance did not reflect similarity in underlying genetic alterations producing resistance. There is thus no tight link between patterns of genetic change and phenotypic diversity, rendering the identification of a genetic locus of homology problematical.

If we do not wish to subscribe to the idea that direct genetic coding for structures or developmental pathways is the locus of homology, perhaps a more general conception of the information content of the genome might do. Van Valen (1982) suggested that homology was "continuity of information" and this definition has been advocated by Roth (1988, p. 2) who applauded its flexibility: "the definition can be used by adherents to any school of thought by simply specifying the relevant kind of information." But this very flexibility means that it is virtually impossible to apply the definition. How are we to judge the information content of two bones in different species? Might this not be especially difficult if we accept that these two bones could have been produced by different developmental processes or even by genes (some of which might differ between the species) with differing patterns of genetic covariance and pleiotropic effect?

E. Connections among Traits as a Locus of Homology

The "principle of connections" has a strong pre-Darwinian pedigree that dates as a formal postulate from the writings of Geoffroy Saint-Hilaire (Appel, 1987), although as a guide for studying the relationships among traits the principle of connections is much older and was advocated by Goethe as a method of comparison (Rieppel, 1988). The idea that it is the pattern of connections among traits that is useful in determining homologies has been advocated by several recent authors, notably Remane (1952) whose criteria for homology have been discussed extensively (e.g. Riedl, 1978). According to Remane

(1952), two structures are homologous if they share similar patterns of connection to other structural elements. Connectivity among structures (by nerves, muscles, bone sutures, ligaments, etc.) is what reveals homology. Even though structures may move relative to one another during ontogeny, they often retain a pattern of connection by dragging with them their innervations and blood supply. The principle of connections has been viewed by several recent authors as an important *a priori* criterion for establishing homology (e.g., Beer, 1980; Golani, 1992; Jardine, 1969; Shubin and Alberch, 1986; Tyler, 1988).

One difficulty with the principle of connections has been establishing a frame of reference within which to analyze interconnections among traits. As Rieppel (1988) shows, if the frame of reference is changed, the pattern of connections among elements changes, leading to a different hypothesis of homology. In order to specify that muscles in two species are homologous because they attach to similarly positioned bones, we need to assume that the frame of reference provided by the bones is both absolute and the reference that serves as a locus of homology. Since no criteria exist for choosing a particular reference framework, there is no nonarbitrary way to decide on homology by connections. Furthermore, all the difficulties with homologizing neural circuits discussed above apply in force to the principle of connections. The implications of particular patterns of connection among neurons in circuits remains unclear, and defining an appropriate framework even to identify a "similar" connection is a daunting task (Harris-Warrick *et al.*, 1992). Indeed, evolutionary patterns in the nervous system may provide the clearest examples of both the difficulty in applying the principle of connections, and uncertainty over the significance of similar patterns of connection (Arbas *et al.*, 1991; Dumont and Robertson, 1986; Striedter and Northcutt, 1991).

F. Synthesis

As is apparent from the discussion above, recent literature on homology is replete with individual authors searching for some key characteristic or combination of characteristics that will allow them to establish homology among characters

and test hypotheses of homology. Much of this literature can be summarized in the form of a multiple choice statement: homologous characters may be (recognized/defined — pick one) by reference to (structure, the nervous system, development, genetics, connections to other characters — pick one or two). The typical approach has been to choose one level of analysis, usually at a level of organization different from the traits under consideration, as the locus of information on the homology of characters in question.

Adoption of one class of data as the key to identifying homologous characters may stem from a desire to have a means of assessing homology independent from phylogeny (e.g., Beer, 1980; Golani, 1992; Goodwin, 1984; Wagner, 1989; also discussed in Donoghue, 1992). If, however, through a detailed examination of two characters by studying their genetics, development, and patterns of connection to other structural features, we could make a determination of probability of homology, then a phylogenetic analysis would be unnecessary: sufficient information would be available from a detailed study of the two traits alone.

If a nonphylogenetic view of homology seems odd nearly 140 years after the publication of *The Origin of Species*, it is increasingly common. Golani (1992), for example, in his analysis of comparative patterns of movement in animals, suggests explicitly that a definition of homology is needed for the comparative study of behavior that avoids reference to phylogeny, and argues that homology is best demonstrated through an analysis of the pattern of connection among behavioral traits in a movement sequence.

On the other hand, while many authors who advocate one particular locus of homology have recognized the importance of common ancestry to the recognition of homology among characters, in practice, phylogenetic considerations often play a small part in analyses of homology: it is *a priori* criteria that are frequently the focus of discussion when a decision is needed on the possible homology of two characters.

It is my view that there is no locus of homology, no class of data or method of examining the details of construction of individual characters that will reveal whether the relationship between two traits is homologous or analogous. Furthermore, I argue below that in order to determine if two characters are homologous, one must analyze the phylogenetic distributions, not only of those characters, but also of many other char-

acters to provide the phylogenetic basis and historical hypothesis specifying the relationships among taxa necessary to interpreting character evolution.

IV. HOMOLOGY AND PHYLOGENY

A. *Phylogeny, Taxa, and Characters*

In this section I present a phylogenetic definition of homology and show how phylogenetic methods can be used to recognize homologous and analogous characters. One consequence of this phylogenetic approach is that *a priori* criteria for examining characters discussed above are relegated to the role of refining observations of similarity among characters and thus our proposals of homology: they do not allow tests of homology or the recognition of homology.

A second key feature of a phylogenetic analysis of homology is that, while the word *homology* may describe a relationship among two (or more) specific characters, the demonstration of that homology requires analysis of many other characters, unrelated to those of immediate interest, because possession of a trait is the property of a taxon. It is the phylogenetic relationships among *taxa* that allow us to assess the homology or analogy of individual *characters*. The criteria discussed above thus differ fundamentally from the phylogenetic approach considered here in focusing on the characters themselves rather than on the taxa possessing them.

Hypotheses of homology may be generated in a large number of ways and the supposition of homology between two characters is logically independent of a phylogenetic test of hypotheses of homology. Although hypotheses of homology are usually based on some prior knowledge of structure or development (and are often founded on "similarity" at some level, recognized by the criteria discussed above), this need not be so. A biologically uninformed observer might easily propose that the wing of an insect is homologous to the wing of a bat, or that the wing of an insect is homologous to the tail of a fish. Either of these hypotheses may be tested phylogenetically to determine the homology (or not) of the characters.

The phylogenetic definition of homology advocated here is based on the approach of Patterson (1982), who suggested

that homologous similarities are those that define natural or monophyletic groups of organisms. If all five species in a clade hypothesized to be monophyletic (on the basis of a phylogenetic analysis of many characters) possess a particular developmental pathway not present in outgroup taxa, then it is most parsimonious to conclude that these species share common development by descent, and that this developmental pathway is homologous in the five species. The similar pattern of development thus is just one of many characters that suggest that these five species are a natural monophyletic taxon (see Brooks and McLennan, 1991; Eldredge and Cracraft, 1980; Fink, 1988; Wiley, 1981).

A character such as a "wing" is not homologous in insects and birds because the character "wing" is not corroborated by other evidence for the monophyly of a taxon that includes birds and insects. That is, there are very few other characters that these two taxa share uniquely that could be used to support the clade insects + birds as a natural taxon. Instead, there are many other characters that suggest a better corroborated phylogenetic hypothesis indicating that birds and insects are each more closely related to other taxa than they are to each other. On this basis, then, we conclude that wings are not homologous in insects and birds.

Figure 1 provides a schematic summary of a phylogenetic approach to homology and analogy. Taxa E, F, G, and H are considered to be a monophyletic clade on the basis of the evidence used to construct the cladogram (for example, a molecular phylogenetic analysis of proteins). Under the pattern of relationships shown in the upper panel, organismal traits 1 and 2 would be considered homologous in taxa E, F, G, and H since it is most parsimonious to assume that the common ancestor of these taxa possessed traits 1 and 2, which then provide further evidence corroborating the natural taxon E, F, G, and H. Trait 3, present in taxa A and G, would not be considered homologous because this trait is incongruent with all the other evidence that suggests that taxa A and G are not each other's closest relatives.

However, if a further study of the relationships of these taxa, perhaps by sequencing more proteins and by combining a previously gathered morphological data set with the molecular data, resulted in a different hypothesis of relationships among the 10 taxa shown (Fig. 1B), then we would have to reevaluate our conclusions about the homology of traits 1, 2,
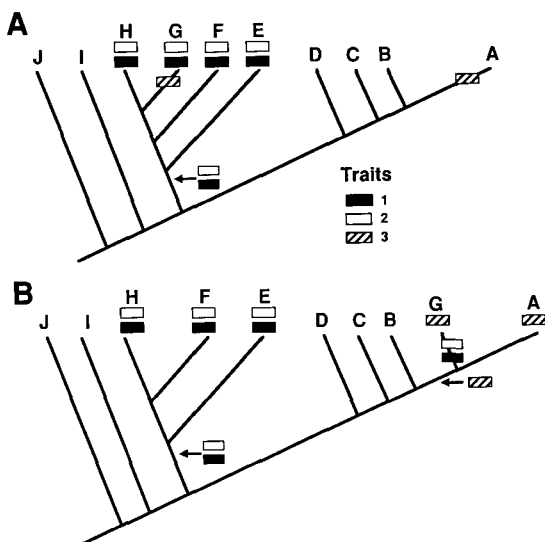
Fig. 1. The phylogenetic definition of homology. (A) Traits 1 and 2 are present in taxa E, F, G, and H and provide evidence that these taxa form a monophyletic clade (arrow). Character 3 is found only in clades A and G. While character 3 does provide evidence that taxa A and G are closely related, this evidence is overwhelmed by the other characters used to make the cladogram in the first place. Each character provides evidence of monophyly for some clades, but it is the distribution of all characters considered together that determines the most parsimonious branching topology. Note that cladograms shown in (A) and (B) are based on a phylogenetic analysis of many additional characters not depicted here. Thus, evidence supporting the branching topology is independent of characters 1, 2, and 3 under discussion here, although these characters could also be included in a phylogenetic analysis of all available data. (B) A suite of new characters has been discovered and a new phylogenetic analysis of all characters now shows that taxa A and G are now considered to be each other's closest relatives. Trait 3 is thus reinterpreted as a homology in taxa A and G and provides evidence that these taxa are a monophyletic clade (arrow). Traits 1 and 2 are still homologous in taxa E, F, and G, but are convergent with traits 1 and 2 in clade G.

and 3. Now, we have increased the amount of evidence we have to support a phylogenetic analysis of the relationships among the taxa and find there is evidence to corroborate taxa A and G as a monophyletic clade. Trait 3 thus contributes to this evidence and would be most parsimoniously interpreted now as homologous between taxa A and G. On the other hand, traits 1 and 2 in taxon G no longer corroborate taxa G, E, F, and H as a monophyletic clade: other evidence outweighs these two characters. Traits 1 and 2 are now considered to be nonhomologous between taxon G and these other taxa, but still would be homologous in taxa E, F, and H. The identification of both analogous and homologous characters thus depends on our estimate of the relationships among taxa. If we were unable to estimate relationships among the 10 taxa shown in Fig. 1, then under a phylogenetic approach to homology and analogy we would be unable to make any statement about the homology of characters present in a subset of those taxa.

A key point in the phylogenetic approach to homology is that the homology or nonhomology of two or more traits does not depend on their similarity to each other (although the initial choice of a character may often depend on a perception of its similarity to another character in a different taxon). A character in two taxa may be very similar structurally, similar in development, have a similar genetic basis, and be similar in function, but might still be nonhomologous (e.g., character 2 in Fig. 1B). It is the relationships among taxa as estimated by an analysis of all the evidence available that allows us to ascertain the homology of characters in those taxa.

B. *Phylogeny, Homology, and Hierarchy*

The hierarchical organization of biological systems has been discussed by many workers (Allen and Starr, 1982; Brooks and McLennan, 1991; Brooks and Wiley, 1986; Gould, 1982; Lauder, 1981; Salthe, 1985; Vrba and Eldredge, 1984) and the implications of a hierarchical view for analyses of homology have received considerable attention. Some authors have asked if the property of homology resides at any one hierarchical level (Roth, 1991). Others, embracing a hierarchi-

cal approach, have questioned whether we can analyze traits across levels by using a single methodology:

> ... methods — such as phylogenetic trees, cladograms and homologies — used for the study of phenomena at one level (say morphology) are generally not applicable to higher-level phenomena (say behavior). (Aronson, 1981, p. 37.)

It is my view that one great benefit of a phylogenetic approach to homology is its direct application to organismal traits of many kinds. Not only are phylogenetic methods applicable to behaviors, developmental sequences, and functions, but some of the most interesting questions in comparative biology arise when we explicitly consider patterns of character homology across hierarchical levels (Lauder, 1990, 1991).

For example, consider the hierarchical arrangement outlined in Table II. If we wish to analyze behavioral traits in several species, we might choose to study a sequence of display behaviors. In order to quantify the display behavior, we could analyze the precise pattern of movements of the head and body during display by measuring kinematic patterns (from films) such as bone excursions, velocities of movement, etc. In addition, we could examine by dissection of preserved individuals the topographic arrangement of muscles and bones of the structures used in the display behaviors. We could also record electrical activity from relevant muscles and thus quantify the pattern of motor output used to generate the behavior. Finally, we might undertake a study of the neuronal circuitry involved in producing the display behavior. While an investigation of all these levels in several species is probably beyond the capabilities of any reasonably finite study, analysis of a few is not (Arbas *et al.*, 1991; Harris-Warrick and Marder, 1991; Katz and Tazaki, 1992; Lauder, 1986, 1990; Paul, 1981a, b, 1991; Reilly and Lauder, 1992; Striedter and Northcutt, 1991).

Given comparative data on characters from several levels (Table II) and a phylogenetic hypothesis of the relationships among species, we can determine the mapping of homologous characters across levels of the hierarchy. As illustrated in Fig. 2, we might find that a display behavior (which appears to be kinematically similar in all species that possess it) has evolved convergently in two groups of taxa. In this case, the display illustrated by taxon H would not be homologous to that in taxa

Table II. One Possible Hierarchy of Levels (Classes) of Characters That Might Be Analyzed Phylogenetically. [a]

Hierarchical level	Example of an organismal trait that might be studied interspecifically
Behavioral	Display behavior during mating
Functional/physiological (at the level of peripheral tissues)	Kinematics of bone movement; physiological properties of muscles; biomechanical tissue properties
Structural (at the level of peripheral tissues)	Topographic arrangement of muscles and bones; tissue histology
Functional/physiological (at the level of the nervous system)	Neuronal spiking patterns; motor patterns; membrane properties; modulation by neurotransmitters
Structural (at the level of the nervous system)	Neuronal morphology; topology of neuronal interconnection; wiring of sensory and motor pathways

[a] Under a phylogenetic approach to the problem of homology it is possible that any definable pair of traits at each level might be homologous no matter what the nature of the traits is. Thus, there is no particular class of characters that serves as a locus of homology.

A, B, and C, despite the fact that behavior in these taxa is not different when we test statistically kinematic variables measured from films of the behavior. In addition, our study of morphology and motor output allows us to ask how homologous components of the mechanistic basis of display behavior relate to patterns of homology (or nonhomology) in the behavior itself. If we find that taxa B and C share a particular morphology and motor pattern (Fig. 2: morphological and motor pattern trait 2) while taxon A retains the primitive morphology and motor pattern (Fig. 2: trait 1) then we can conclude that taxa B and C possess an underlying mechanistic basis for the display behavior that is not homologous to that in taxon A. That is, the behaviors are homologous within clade A, B, and C but the morphological and motor substrates for the behaviors are not. In fact, according to the pattern shown in Fig. 2, taxon A has retained a primitive morphology and is convergent to taxon H not just in possessing the behavior, but also in the physiological basis for the behavior. Taxa D, E, F, and G possess an homologous morphological framework, but lack characters at the behavioral level: these species never evolved a display although they possess the requisite musculoskeletal structure. Phylogenetic patterns similar to those depicted in Fig. 2 are increasingly being demonstrated as comparative studies of the physiological and neural basis of behavior become more common (Katz and Tazaki, 1992; Lauder, 1990, 1991, 1993; Paul, 1991; Reilly and Lauder, 1992; Shultz, 1992; Striedter and Northcutt, 1991).

Study of the phylogenetic patterns of congruence among classes of characters at different hierarchical levels raises several general issues: 1), do some levels tend to be more conservative than others and show relatively little interspecific variation? 2), are traits at some levels more interspecifically labile and if, so, is this variation correlated with variation at another level?

Many interesting problems in the evolution of organismal design may appear where there is discordance among levels. For example, taxa in a monophyletic group might show homologous phenotypes produced by divergent developmental pathways. Or, taxa may show homologous patterns of muscle activity, but divergent behaviors because of alterations in musculoskeletal topology (Lauder, 1991). Combination of the phylogenetic definition of homology with an analysis of organ-

ismal traits at several hierarchical levels allows these issues to be addressed.

Many other types of hierarchical arrangements might be considered. Analysis of an ecological hierarchy (individuals, populations, communities, and biogeographic regions), for example, might provide a basis for examining how homologous ecological characteristics of two taxa relate to traits at other levels such as morphology or life history patterns (Brooks and McLennan, 1991). Or, we might wish to analyze a genetic/developmental hierarchy (Atchley and Hall, 1991; gene sequences, patterns of genetic covariation, epigenetic pathways, phenotypes) to discover how traits at these different levels covary phylogenetically and how homologies at one level map onto homologies at other levels.

While such approaches are still in their infancy (in part because of the view that many classes of characters are not able to be analyzed using phylogenetic methods), I believe that the historical analysis of different types of traits and the con-
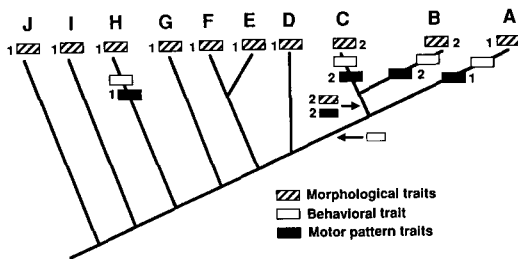

Fig. 2. Schematic illustration of a phylogenetic analysis of hierarchical characters showing how kinematically similar behaviors might be produced by different "underlying" motor patterns and structures. A behavioral trait (a display behavior, for example) is common to taxa A, B, and C and is homologous within these taxa (arrow), while the behavior in these three taxa is convergent with the similar behavior in taxon H. Motor pattern 1 is also convergent between taxa H and A. However, taxa B and C have acquired novelties in motor pattern and morphology (arrow at the internode leading to taxa B and C), so that the behavior homologous to that in taxon A is now generated by nonhomologous morphological and functional characters. Taxon A retains the primitive morphology.

comitant recognition of homologous traits at different levels
will lead to the discovery of new and interesting patterns of
association among characters that will guide future mecha-
nistic investigations.

C. Phylogeny and Iterative Homology

Although *serial homology* [one form of *iterative homology*
(Ghiselin, 1976)] has been an active topic of discussion in the
homology literature since the time of Owen (Appel, 1987;
Minelli and Peruffo, 1991; Patterson, 1982; Rieppel, 1988),
recently Roth (1991) and Wagner (1989) have argued that a
"biological homology concept" is needed in part because a
phylogenetic approach to homology does not allow iterative
traits in organisms to be homologous (Patterson, 1982).
I suggest that a phylogenetic approach to homology can
easily deal with the reality of repeated traits within organisms,
and thus argue that there is no necessity for a separate biolog-
ical homology concept. In my view, iterative homology simply
refers to homology of one or more developmental processes (or
patterns of genetic covariation) at a greater level of phylo-
genetic generality than the individual organism. To say that
cervical vertebra 4 is serially homologous to cervical vertebra 5
in an individual mammal is simply to say that species in the
Mammalia share an homologous developmental pathway (or
set of pathways) that produces serially arranged phenotypic
structures similar in size and shape.
Figure 3 illustrates schematically how one might interpret
"serial homologues" among several Recent taxa in a phylo-
genetic context. Taxon A might be argued on a biological
homology concept to possess three serially homologous body
segments. But such a statement represents a confusion of
phenotypic pattern within an individual with interspecific
(phylogenetic) differentiation in developmental/genetic pro-
cesses. Seen in the context of its phylogenetic relatives, taxon
A (Fig. 3) possesses a phenotypic condition of three repeated
body segments that results from sharing an homologous nov-
elty in developmental/genetic pattern with taxon B. Similarly,
taxa A, B, and C share another (homologous) develop-
mental/genetic novelty that gave rise to repeated segments in
comparison to outgroup taxa D and E. At an even more

general level, taxa A to E possess an homologous appendage on the first body segment due to novelties in development that arose in the lineage leading to the monophyletic clade A to E. The phenotypic condition of individuals in taxon A ("serial homology") thus results from a nested set of derived homologous developmental and/or genetic characteristics. It is not particularly enlightening, then, to refer to an individual in taxon A as possessing serial homology, as the components of the phenotypically repeating pattern have different phylogenetic histories that characterize increasingly inclusive monophyletic clades of taxa.

A less schematic example illustrating the above point concerns vertebrate pectoral and pelvic appendages. On the basis of a phenotypic analysis of extant tetrapod taxa one might wish to conclude that forelimbs and hindlimbs are
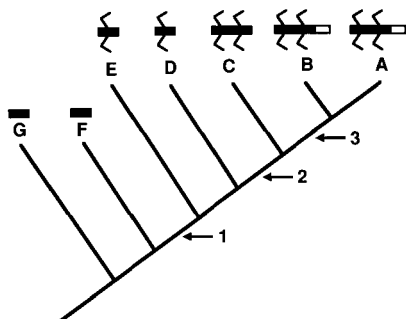

Fig. 3. Schematic illustration of how the phylogenetic definition of homology may be applied to serially homologous structures within a taxon. "Serial homology" of structures within individuals of taxon A actually reflects nested phylogenetic sets of homologous developmental and genetic novelties that define monophyletic clades. Three are shown here. Outgroup taxa (G and F) possess a single body segment with no appendages. Novelty 1: alterations in development generate a bilaterally paired appendage on the body. Novelty 2: acquisition of developmental/genetic programs (perhaps as a result of gene duplication) generate a repeated element of structural design — a second body segment. Novelty 3: further alterations in developmental/genetic processes generate a third body segment with no appendages.

serially homologous: both appendages typically possess a single proximal segment, two middle bony elements, a collection of smaller carpal or tarsal bones, and distal phalanges. Indeed, the phenotypic resemblance between fore- and hindlimbs in tetrapods is striking, and the limbs are similar in developmental characteristics also [suggesting to Roth (1984) that the forelimb and hindlimb are homologous in derived tetrapods].

But a phylogenetic analysis reveals that the pectoral and pelvic appendages in early vertebrates do not possess such detailed similarities in structure. Sharks and ray-finned fishes possess pelvic fin supports that are quite different in morphology from the endoskeletal elements supporting the pectoral fin (Jarvik, 1980). In *Amia*, for example, pelvic fin supports consist of a single dominant pelvic bone on each side supporting a collection of radial bones and cartilages, while the pectoral fin is supported by an elongate set of proximal radial bones, each of which articulates with a small distal radial and a large medial basal cartilage. In more derived ray-finned fishes, where the pectoral and pelvic girdles may attach to each other, there is even less morphological resemblance (Stiassny and Moore, 1992). In sharks, numerous radials articulate with pterygial cartilages in both girdles, but the number and nature of these articulations vary between the girdles.

In sharks and primitive ray-finned fishes the existence of repeated radial elements in each appendage may indicate some general level of common developmental/genetic programs for development, but these commonalities do not extend to the details of appendage construction itself. Ray-finned fishes, on the basis of the phenotypic evidence, would appear to have even less in common between pectoral and pelvic appendages.

With the origin of tetrapods and the common functional role for fore- and hindlimbs in terrestrial support and locomotion, however, developmental/genetic links between fore- and hindlimbs appear to have arisen that constitute a homology for tetrapods. The precise nature of the common developmental and genetic mechanisms that give rise to similar phenotypes in tetrapod limbs is not known, but there is ample quantitative genetic evidence (reviewed in Lande, 1978) to suggest that limb design is polygenic and that "limb genes" have many pleiotropic effects on other morphological features; see Chapter 6. It is not structural similarities in the fore- and

hindlimbs of a single individual that constitutes an homology, nor is the similarity in developmental mechanisms between fore- and hindlimbs evidence of "serial homology." Rather, the homologous traits within tetrapods are the shared developmental programs and patterns of genetic covariance that characterize a monophyletic clade of taxa, the Tetrapoda.

On the basis of the comparative anatomy of the limbs in lungfishes, "rhipidistians," and early amphibians it is likely that the developmental homologies and patterns of genetic covariation that characterize tetrapod limb development arose in a series of stages and not suddenly with the origin of terrestrial life. The pelvic and pectoral appendages of *Eusthenopteron*, while similar in general pattern, possess several distinct structural features (Jarvik, 1980), while those of early amphibians show greater structural similarities in possessing a single proximal element and two larger elements that articulate distally (Coates and Clack, 1990).

Lungfishes, primitive ray-finned fishes such as sturgeons, and sharks, all possess pectoral and pelvic fins with a general structural plan in common, but only lungfishes, "rhipidistians," and tetrapods appear to share a common pattern between the two appendages of having a single proximal element articulating with the supporting girdle, and a greatly reduced number of distal elements articulating with that proximal element. A model of increasing common genetic control of both appendages prior to the origin of tetrapods at least is consistent with the phenotypic evidence, suggesting that developmental and genetic covariation between pectoral and pelvic appendages existed in taxa that were primarily aquatic, prior to the origin of tetrapods.

This scenario suggests an experiment: test for common patterns of development and genetic control (via quantitative genetic and selection experiments) in taxa such as fishes, where crosses can be easily made, and compare the covariance between fore- and hindlimb elements with the results of similar experiments in tetrapods. The prediction is that a much higher degree of correlated response to selection will be found in tetrapod limbs than in the appendages of fishes, reflecting the homologous developmental/genetic control mechanisms that may characterize many tetrapod clades.

V. HOMOLOGY AND FUNCTION

The study of function has not received much attention in systematic and comparative biology, and when it has the focus has tended to be negative (Lauder, 1990). Physiological functions have been viewed as labile, of little utility in comparative studies, and difficult to define and thus analyze. Table III provides a sampling of literature sentiment on the possibility of studying functional homology, and the consensus is not optimistic. One key issue that underlies most views of function is the proposed intimate relationship with structure: "Functions are clearly inextricably tied with the structure of the features that perform them" (Tyler, 1988; Table III).

One difficulty with this view is that functions may be tied to structure at a different hierarchical level than one might at first think (Lauder, 1990, 1993). For example, if we consider as a possible physiological function the pattern of electrical activity in a muscle, the structural substrate for this function might lie in the connections among neurons in the spinal cord, or it may be more abstract than that, lying instead in the membrane properties and sodium channels of nerve cells in the circuit (Table II). Given the increasingly abstract conceptualizations of what constitutes a structural circuit in neurobiology (Getting, 1988; Harris-Warrick *et al.*, 1992), it is difficult to understand how we can tie many functions to a structural substrate in a simple fashion. I have criticized elsewhere the view that functions are necessarily more labile than structures (Lauder, 1990, 1991). Statements on the lability of function are most commonly based on our preconceived notion that structure is solid, repeatedly observable, and definable, rather than on quantitative analyses of interspecific patterns of both structure and function.

The purpose of this section is to develop a brief case study of the evolution of structure and function to illustrate the issues discussed above. In particular, this case study of muscle morphology and function in ray-finned fishes (Actinopterygii) will be used to depict (1) the initial proposal of homology, (2) the determination of the homology of muscles, (3) an analysis of muscle function and of functional homology, and (4) phylogenetic congruence between structural and functional characters and the implications of congruence (or the lack thereof) for the recognition of homology. I will use the phylogenetic definition of homology outlined above as a tool to

Table III. Selected Statements from the Literature Commenting on the Possible Homology of Organismal Functions

Reference	Comment on organismal function and homology
1. Haas and Simpson (1946, p. 323)	"Functions, considered as abstractions and without consideration for the structures that perform these functions, should not be spoken of as homologous."
2. Atz (1970, p. 60)	it is "...impossible for nonhomologous structures to have homologous functions."
3. Riedl (1978, p. 248)	"The contraction of a biceps naturally stands beyond the limit of homology."
4. Ross (1981, p. 2157)	"Certainly, functions have phylogenetic histories but it seems that the rules are different from those which governed the patterns of evolution depicted in the familiar phylogenetic trees."
5. Tyler (1988, p. 344)	"Homology applies most appropriately to the structural features, not their functions."
6. Burggren and Bemis (1990, p. 197)	"One reason why physiologists have problems with homology is that there are no easy means to assess the homology of the quantitative features of greatest familiarity and interest to physiologists except by reference to the morphological substrates of these functions."
7. Wake (1991, p. 323)	"... many workers have difficulty accepting functional characters, both because they believe that the underlying morphology must be sought, and that morphology then provides the characters appropriate to phylogenetic analysis and because functions are viewed as associations of several potential characters ...."

examine patterns of evolution at different hierarchical levels, and to suggest new research questions in the evolution of muscle structure and function.

A. Case Study: The Evolution of Muscle Function in Ray-Finned Fishes

In 1973, D. E. Rosen, elaborating on the previous work of Holstvoogd (1965) and Nelson (1969), adduced evidence that the Neoteleostei constituted a monophyletic clade of teleost fishes. Rosen's proposal of monophyly for this clade was significant because the neoteleost fishes comprise more than half of the 24,000 species of teleost fishes, and evidence of monophyly for such a large clade represented an important step in understanding the phylogeny of fishes (Lauder and Liem, 1983). One of the characters used by Rosen (1973) was the presence of the retractor dorsalis muscle (RD) in the pharyngeal region of neotelosts. This muscle is proposed to be homologous within neotelosts (Fig. 4A) because of its consistent origin from the vertebral column and insertion on one or more of the upper pharyngeal bones (Fig. 4B): i.e., because of similarity in position and connection to surrounding elements. Because a number of other characters also corroborate the Neoteleostei as a monophyletic clade (see Johnson, 1992; Lauder, 1983b; Lauder and Liem, 1983; Stiassny, 1986), I consider the presence of a retractor dorsalis muscle to be homologous within neoteleosts (Fig. 4A) under a phylogenetic definition of homology.

However, as has been noted by a number of workers (e.g., Allis, 1897; Nelson, 1969), several other clades of ray-finned fishes also possess a muscle that appears to be very similar to the neoteleost retractor dorsalis. For example, gar (*Lepisosteus*, in the Ginglymodi) and bowfin (*Amia*, in the Amiidae) also possess a muscle that takes its origin from the vertebral column and inserts on the upper pharyngeal jaw bones (Fig. 4C). On the basis of a criterion of similarity of structure and connection to surrounding elements, one might propose that the retractor dorsalis muscle in *Amia* and *Lepisosteus* is homologous to that of neoteleost fishes. But this hypothesis is refuted by the host of other characters supporting a phylogeny in which the clades containing *Amia* and
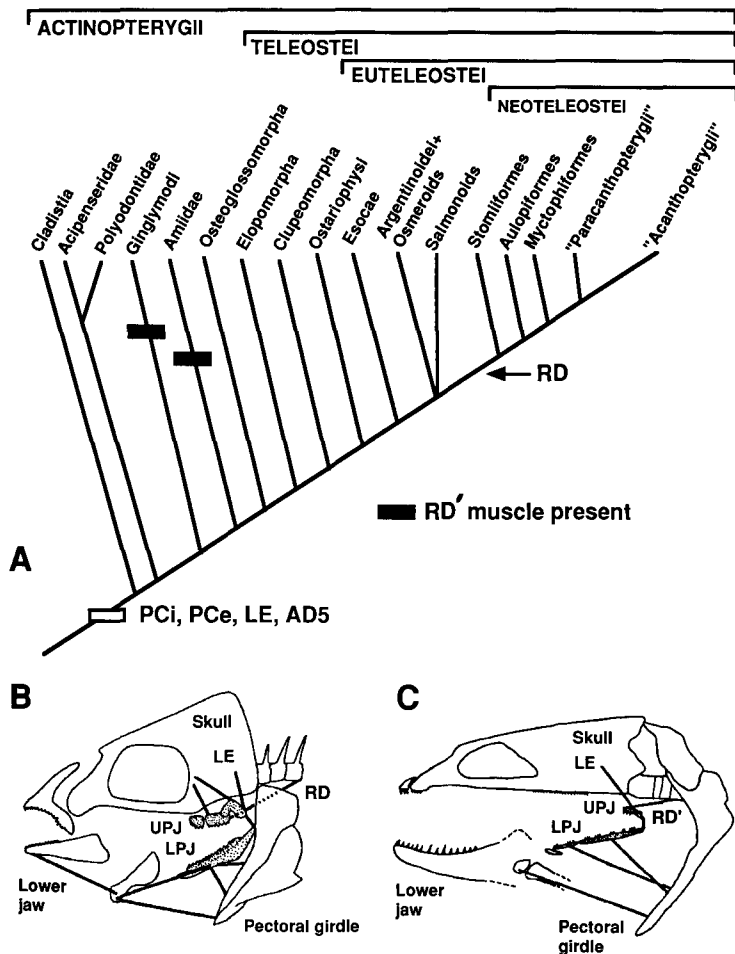
Fig. 4. (A) A greatly simplified diagram of phylogenetic relationships of the major clades of ray-finned fishes to illustrate the independent evolution of a dorsal retractor muscle (RD, arrow; and RD', black bars) in the Neoteleostei, Amiidae, and Ginglymodi. Note that many Recent and fossil clades have been omitted for clarity. A number of pharyngeal muscles are primitive for ray-finned fishes, including the pharyngo-cleithralis internus and externus (PCi and PCe), the external levators (LE), and the fifth branchial adductor (AD5) (Lauder

and Wainwright, 1992). A dorsal retractor has also been found in several other ray-finned fish species, although the phylogenetic position of these taxa does not affect this discussion of the convergent retractor muscle. (B) Schematic illustration of the skull in a derived ray-finned fish such as a member of the sunfish family Centrarchidae (in the "Acanthopterygii"). The RD muscle originates on the vertebral column and inserts on the upper pharyngeal jaw (UPJ). (C) Similar diagram of *Amia* to show the convergent retractor muscle (RD') extending from the vertebral column to the upper pharyngeal jaw. LPJ, Lower pharyngeal jaw.

Lepisosteus are not closely related to neoteleost fishes (Lauder and Liem, 1983; Nelson, 1969; Wiley, 1976).

This phylogenetic interpretation is illustrated in Fig. 4A, in which the neoteleost RD is considered as a homology for that clade, while *Amia* and *Lepisosteus* are labelled as possessing a nonhomologous dorsal retractor muscle, labelled RD'. It is highly unparsimonious to conclude that the "dorsal retractor muscle" in *Amia, Lepisosteus,* and neoteleosts is homologous. Under that scenario, all the characters that neoteleosts share would have to have been lost in *Amia* and *Lepisosteus,* and all the characters shared by the nested sets of clades within the Teleostei that branch off prior to the Neoteleostei (Fig. 4A) would also have to have been lost in *Amia* and *Lepisosteus.*

There are approximately seven extant species of gars in the Ginglymodi (Wiley and Schultze, 1984), and I interpret the RD' as homologous among these species. However, it is not possible to decide if the RD' is homologous in *Amia* and *Lepisosteus* (Lauder and Wainwright, 1992): the RD' muscle might have arisen once below the Ginglymodi and been lost in teleost fishes (two evolutionary "steps," in which case the RD' would be homologous in *Amia* and *Lepisosteus*) or it might have originated independently in these two clades (also two steps, indicating that the RD' is not homologous in *Amia* and *Lepisosteus*).

Given this structural pattern, what might we find if the function of the RD, RD', and surrounding muscles is investigated? Does structural homology imply functional homology, and thus that the RD and other muscles considered to be homologous within neoteleosts will possess homologous func-

tions? Are some levels of the hierarchy illustrated in Table II more phylogenetically conservative than others? In order to propose functional homologies, we need to investigate the function of pharyngeal muscles in several ray-finned clades. By recording muscle activity patterns, using the technique of electromyography, a precise description of when each pharyngeal jaw muscle is active relative to others can be obtained (Lauder, 1983a,b; Lauder and Wainwright, 1992).

Figure 5 illustrates representative patterns of pharyngeal muscle activity in derived neoteleosts from the Family Centrarchidae (Fig. 5A and B: *Lepomis*, *Ambloplites*) and from *Lepisosteus* and *Amia* (Fig. 5C and D). Note that the RD' muscle possesses a grossly similar activity pattern in *Lepisosteus* and *Amia* in that the bulk of RD' activity occurs following activity of the AD5 muscle. In *Amia*, however, the levator externi muscles (LE3/4) are active during swallowing while homologous muscles in *Lepisosteus* are not (the levatores externi muscles are primitively present in ray-finned fishes). If the pattern of muscle activity in a neoteleost such as *Ambloplites* is compared to that of *Amia*, the levatores externi and retractor muscles appear to be active at similar relative times (Lauder and Wainwright, 1992).

Recordings such as those shown in Fig. 5 (also see Lauder, 1983a,b, 1993; Lauder and Wainwright, 1992) for a variety of ray-finned fish clades suggest the following three representative functional characters for consideration. (1) Activity of the posterior levator muscles originates prior to and significantly overlaps activity in the retractor muscle. (2) Onset of activity in the fifth branchial adductor (AD5) occurs prior to onset of activity in the retractor muscle during a swallowing cycle. (3) Activity in the pharyngocleithralis externus (PCe) muscle is present during prey swallowing and significantly overlaps activity in the retractor muscle.

Examining the phylogenetic distribution of these functional characters on the simplified phylogeny of ray-finned fishes shown in Fig. 4 indicates that three conclusions regarding the homology of pharyngeal motor patterns can be drawn.

First, *Lepisosteus* and *Amia* differ in the timing of activity of the external levator muscles with respect to the RD' muscle. *Amia* has a motor pattern similar to that in sunfishes, while *Lepisosteus* shows little activity in the posterior levators during swallowing. Under a phylogenetic definition of homology, this aspect of the motor pattern in *Amia* is convergent (anal-
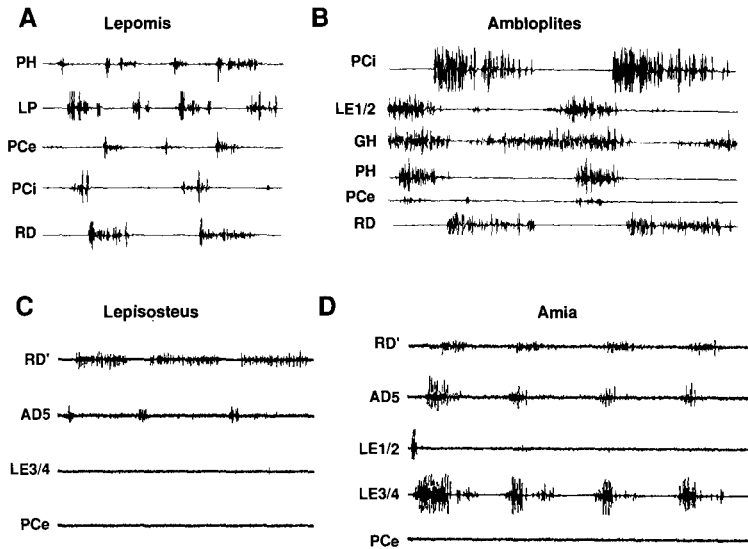
Fig. 5.　Patterns of muscle activity in four taxa of ray-finned fishes. (A) and (B) show motor patterns in two genera of sunfishes (Centrarchidae: Acanthopterygii). (C) and (D) show muscle activity in two nonteleost ray-finned fishes: *Lepisosteus* (Ginglymodi) and *Amia* (Amiidae). The RD' muscle in *Amia* and *Lepisosteus* is convergent with the RD of *Lepomis* and *Ambloplites*. Abbreviations: AD5, fifth branchial adductor; GH, geniohyoideus; LE, levator externus muscles (either 1 and 2, or 3 and 4); LP, levator posterior muscle, one of the external levator series; PCe, pharyngocleithralis externus; PCi, pharyngocleithralis internus; PH, pharyngohyoideus; RD, retractor dorsalis muscle of neoteleostean fishes; RD', the dorsal retractor muscle of *Amia* and *Lepisosteus.*

ogous) to that of neoteleosts, while *Lepisosteus* is uniquely derived in this character. Thus, despite structural homology of the external levator muscles in ray-finned fishes there has been considerable evolutionary differentiation at a functional level.

　　Second, both *Lepisosteus* and *Amia* possess relative timing of the AD5 and RD' muscles similar to that between the AD5 and retractor dorsalis (RD proper) in neoteleostean fishes.

phylogenetically, then, these taxa are convergent in sharing a similar (but not homologous) motor pattern.

Third, *Amia* and *Lepisosteus* share a lack of activity in the PCe muscle during swallowing, and are divergent from neoteleostean fishes which possess such activity. However, within the neoteleostean fish family Centrarchidae, the genus *Ambloplites* differs from the other closely related sunfish taxa studied to date in the timing of PCe activity relative to the RD (Fig. 5A and B; Lauder, 1983a,b). Thus, despite structural homology of the PCe and RD within the Centrarchidae, there has been divergence at the functional level.

Comparison of activity patterns in structurally homologous branchial muscles among the three major clades of percomorph teleosts (a large derived neoteleostean clade within the "Acanthopterygii"; Fig. 4A) that have been studied to date (the Centrarchidae, Cichlidae, and Haemulidae) shows that numerous functional specializations have occurred in the activity patterns of homologous muscles. For example, in haemulid fishes, the sternohyoideus muscle is strongly active during prey transport (Wainwright, 1989a,b) while activity is never seen in the sternohyoideus muscle during prey transport in centrarchid fishes (Lauder, 1983a,b). Phylogenetic differentiation in muscle function (motor output) among percomorph fish clades has thus occurred within a structurally homologous muscular framework.

Results of this case study are typical in illustrating the complexity of the relationship between structure and function obtained when one measures functional characters and compares their distribution to associated structural features (Lauder, 1990, 1993). At the same time, in the course of past work on the evolution of muscle function in ray-finned fishes, several extremely conservative functional characteristics have been identified as retained despite extensive reorganization of musculoskeletal topology (Lauder, 1990, 1991; Wainwright and Lauder, 1992). Both structures and functions may be conserved phylogenetically, and both types of characters are capable of extensive transformation.

B. *Synthesis: Homology and Function*

While Riedl (1978) has suggested explicitly that muscle contraction may not be analyzed using the concept of homology (Table III), I would argue that a definable pattern of muscle activity is an organismal trait just like any structural feature. Just like a structural character, functions may be considered homologous if they characterize a natural, monophyletic clade of taxa. So, the common pattern of activity in the AD5 muscle in *Amia* and neoteleosts is one character providing evidence, along with the presence of a dorsal retractor muscle, that neoteleost fishes and *Amia* are a monophyletic clade. But I reject this hypothesis because there are many other characters that support a different grouping of monophyletic clades — that shown in Fig. 4A. If further characters came to light indicating that the most parsimonious interpretation of all characters bearing on ray-finned fish phylogeny shows *Amia* to actually be a neoteleost, then I would reverse my interpretation of the RD' and muscle activity characters, and conclude them to be homologous between *Amia* and sunfishes. The claim of homology (in this case of a functional character) stands or falls on the basis of the phylogeny as a whole.

A corollary of the phylogenetic approach to analyzing organismal traits is that even if further investigation showed that the RD' of *Amia* and neoteleosts has a very similar pattern of development, and even if it was shown that the genes producing these muscles were homologous and present in all ray-finned fishes, I would still regard the phenotypic structure of a retractor muscle (and related motor patterns) as convergent between *Amia* and neoteleosts.

The approach taken here — examining the distribution of muscle structure and function on a phylogeny of ray-finned fishes — suggests a number of avenues for further study. In particular, if muscle activity patterns are convergent among *Amia, Lepisosteus*, and neoteleosts, are the neural circuits that produce the motor pattern similar in structure? In other words, does convergence at one level of the hierarchy of Table II (muscle structure) entail convergence at other levels? In addition, in cases within neoteleosts where structurally homologous muscles are shown to possess analogous (convergent) functional traits, one might ask if the neural circuitry that generates the motor output has been conserved

phylogenetically, or which aspects of the circuit have changed — the wiring pattern, or perhaps neuromodulators or membrane properties. Finally, if changes have occurred in muscle structure and function, what does this imply for the behavioral (kinematic) level? Are the observed behaviors generated by analogous muscles and their functions similar too? As I have discussed elsewhere, interspecific changes in musculo-skeletal design and function may still produce identical behaviors and, conversely, a change in behavior may result from changes at any of several hierarchical levels (Lauder, 1991). Understanding the diversity of transformational patterns among hierarchical levels and the mechanistic bases for these patterns is a major challange for the future.

VI. CONCLUSIONS

My goals in this chapter are twofold. First, I wish to demonstrate the prominent role that *a priori* criteria for the recognition of homology have played in the literature. Despite wide recognition that the concept of homology has strong phylogenetic underpinnings, much of the recent homology literature is devoted to considering the extent to which one nonphylogenetic criterion or another provides information on the homology of characters. The promise of such an approach is that the homology or analogy of organismal traits might be determined by a detailed examination of the characters themselves, without reference to the phylogenetic distribution of the characters in ingroup and outgroup clades. There is a clear trend in the literature to divorce the definition and recognition of homology from a phylogenetic basis (Beer, 1980; Golani, 1992; Goodwin, 1984; Roth, 1991).

Second, in the context of presenting a phylogenetic definition of homology and of providing an example of the analysis of structural and functional homology in the musculoskeletal system of ray-finned fishes, I suggest that the search for a "locus" of information on character homology is misguided. Such searches actually provide data on the similarity of characters we might use in proposing an hypothesis of homology. This proposal is then tested via an explicit phylogenetic analysis which examines the distribution of characters on a phylogeny and estimates the relationships of taxa. The result of the phylogenetic analysis alone determines if two characters

are homologous. In the absence of a phylogenetic analysis, one can only propose homologies based on character similarity; one cannot test hypotheses of homology. It is interesting to note that, in the literature advocating a particular class of data as a locus of homology, that locus is most often claimed to reside at a different hierarchical level than the traits under consideration. The class of data that is proposed to contain homological information on a phenotypic trait (e.g., development, genetic data, the structure of the nervous system) is often relatively inaccessible and limits the utility of such a *priori* criteria for contributing to an understanding of historical patterns to different types of traits.

The adoption of an explicitly phylogenetic definition of homology leads naturally to the analysis of congruence among hierarchical classes of characters: if no one level or class of traits serves as a locus of homological information, then all may be equally subject to historical analysis. For example, how congruent are behavioral changes in a clade with morphological and physiological features involved in the production of those behaviors? How congruent are developmental pathways and epigenetic associations with the phenotypic end products of those processes? How concordant are patterns of genetic correlation in life history traits among taxa with homologous ecological or trophic patterns? I regard the documentation of patterns of historical concordance and divergence among classes of data, levels of organization, and developmental, genetic, and physiological processes as one of the most exciting areas of investigation in organismal biology.

Since we lack even a modest number of case studies of this type, it is still unclear what patterns will emerge and what kinds of causal hypotheses will be suggested by the results of such phylogenetic analyses of behavior, function, development, and genetics. The analysis of the mechanisms driving patterns of character association is a virtually untapped field that may well be a future focus of comparative biology.

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