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Homology, Analogy, and the Evolution of Behavior

George V. Lauder

ANY comparative study in biology of necessity involves some attempt to assess similarities and differences among organisms. These similarities and differences may be interpreted within two general frameworks: (1) an *equilibrium* view in which behaviors or morphologies are viewed in relation to the environment and explanations of similarities and differences are sought in terms of selection forces and environmental variables, and (2) a *transformational* view where patterns of similarity and difference among organisms, species, and higher taxa may be used to construct evolutionary sequences. The transformational approach (Lauder, 1981) focuses on historical patterns of structure, function, and behavior, and relies fundamentally on phylogenetic hypotheses to provide a basis for interpreting historical sequences and testing evolutionary concepts. The subject of this volume is the evolution of behavior, and in this chapter I will focus on historical interpretations of similarities and differences in behavior, and on methods for analyzing evolutionary patterns of behavior.

There has been an interest in transformational patterns of behavior and in the comparison of behaviors in relation to the phylogenetic relationships of species from the early days of ethology (Heinroth, 1911; Whitman, 1899). Lorenz (1950, p. 238), for example, remarked that "as early as 1898, C. O. Whitman wrote the sentence that marks the birth of comparative ethology. 'Instincts and organs are to be studied from the common viewpoint of phyletic descent.'" However, most ethologists in the last twenty years have focused on the relationship of behavior to the environment inhabited by organisms, and this focus is well exemplified by the papers in this book (e.g., Fitzpatrick and Woolfenden, Thornhill). The dominant emphasis of ethologists has been on the physiological basis of behavior (see Fentress, 1976; Manning, 1967)

and on the equilibrium relationship of behaviors to fitness, selection pressures, and environments. For example, Manning (1967, p. 1) opens his text on animal behavior with the statement that "there are two main approaches to the study of behavior, the physiological and the psychological." A survey of a number of texts in ethology reveals that only two (Alcock, 1975; Eibl-Eibesfeldt, 1970) even list the words "phylogeny" and/or "homology" in the index (e.g., Manning, 1967; Marler and Hamilton, 1966; Hinde, 1966; Bateson and Hinde, 1976; Gould, 1982). Evolution of behavior usually means the study of animal behavior in relation to the environment and the identification of possible selective explanations for the distribution of behaviors within and among species.

Despite the emphasis on equilibrium analyses in ethology, a number of investigators have considered the historical and transformational implications of similarities and differences in behavior among organisms. Among the larger volumes on this topic, the books edited by Roe and Simpson (1958), Brown (1975), and Masterton et al. (1976) stand out as offering the most detailed treatment of ethology in a transformational framework. It is apparent from these books that a fundamental issue in historical ethology, the problem of homology recognition, has yet to be satisfactorily resolved. Concepts of homology and convergence are fundamental to the study of any historical pattern and to the testing of historical explanations in ethology. If ethology is to discern evolutionary patterns of behavior and if it is to contribute to generalizations about the process of evolution and to the recognition of patterns in nature, then it is important to critically evaluate conceptual approaches to the study of historical ethology.

In this chapter I attempt to clarify the issue of homology in ethology by focusing on two classes of criteria that have been proposed by ethologists as reliable indicators of behavioral homology: morphological and neural correlates of behavior. I begin by presenting an overview of historical analyses by ethologists and by reviewing proposals that homologous behaviors can be recognized by analyzing morphological and neural substrates of behavior. Of special importance for this paper are the following questions: (1) Are current research methods in ethology adequate for the analysis of historical patterns and transformational sequences of behavior? (2) Do a priori criteria often used by ethologists provide a useful method for determining behavioral homologies? (3) What are alternative approaches to the analysis of historical patterns and the recognition of behavioral homologies? and (4) How tightly coupled are historical patterns of morphological, neural, and behavioral features? Finally, I conclude with a case study that is used to illustrate one approach to the analysis of behavioral evolution. I know of no other such study where the evolution of a behavior has been studied comparatively (at the species level) within a clade at morphological, physiological, and ethological levels. This case study will

serve as an example of an analysis of the historical relationship among behavioral, functional, and morphological characters, and will provide the basis for proposing hypotheses about the evolution of behavior and the evolutionary transformation of motor patterns.

HISTORICAL ANALYSIS IN ETHOLOGY

Common Research Approaches

Ethologists have several approaches to historical issues. Those issues of special interest in the context of a discussion of homology in ethology are:

1. The use of behavioral characters to produce phylogenies of organisms.
2. The use of ethological series as a basis for scenarios about the evolution of behavior.
3. The identification of homologous behaviors by the application of a priori criteria (i.e., criteria independent of phylogenetic patterns of character distribution). Of primary concern here is the concept that the structure of the nervous system producing the behaviors of interest and the morphology used in a behavior provide *prima facie* evidence for behavioral homology.

Before discussing these three issues, it is necessary to clarify the use of three terms that are important for this analysis. First, consider the terms "function" and "behavior." While some ethologists claim that their criteria for behavioral homology are drawn from the work of morphologists (e.g., Atz, 1970; Tinbergen, 1959; Eibl-Eibesfeldt, 1970), their use of the term "function" is very different from that of evolutionary morphologists. Cracraft (1981) noted the difference between function and behavior as concepts useful in studying historical patterns, and commented that "functions of structures generally have not been thought of as systematic characters, whereas ritualized behavior patterns have been utilized as characters for many years. . . . It is the behavior pattern, then, and not the function that constitutes a systematic character." Cracraft's use of the term "function" is consistent with that of most evolutionary morphologists: functions are the actions or uses of structures. But ethologists, in keeping with the dominance of equilibrium methods and the emphasis on environmental variables as determinants of behavior, have generally held that function "definitely means something quite different and specific: it means 'selective advantage'" (Hailman, 1976b, p. 184). Other ethologists have expressed similar views: "A function is a beneficial consequence of a behavior" (Bertram, 1976). "Within ethology, questions of function have been studied

in two main ways: comparative studies of related species in which interspecies variations in a character are related to environmental variables . . . and detailed field studies involving either field experiments or the assessment of relations between variability in a trait and subsequent survival or reproductive success . . ." (Bateson and Hinde, 1976, p. 193). "A primary aim of primate socio-biology (or socio-ecology) is to explain variation in social behavior in terms of biological function. To do this, it is necessary to consider the possible consequences of differences in behavior. . . . Some of these may be selectively advantageous, some neutral and some disadvantageous. Through this paper we refer to those in the first category as 'functions'" (Clutton-Brock and Harvey, 1976, p. 195). The ethological definition of function is similar to what Rock and von Wahlert (1965) called "biological role." In this chapter I will use the term "function" in its morphological sense. This avoids the numerous difficulties associated with determining selection forces before one can meaningfully use the term "function." In addition, the morphological definition will allow us to consider a methodology for historical analysis in which behaviors, morphologies, and functions can be used both as systematic characters and as elements of an overall transformational pattern with general implications about the evolution of behavior.

Secondly, consider terms that could be applied to features of organisms that are mistakenly believed to be homologous. Patterson (1982, p. 45) distinguishes five possible terms that represent nonhomologous (homoplasous) features: parallelism, convergence, analogy, mimicry, and chance. To this list we might add learned similarities. I will include the last four terms of Patterson's list and learned behavioral similarities under the label "convergence." Thus, my use of the word "convergent" includes nonhomologous features that may be the result of several processes.

1. Behavioral characters and phylogeny. Perhaps the most common avenue of research into historical problems in ethology is the use of behavior to clarify the relationships of organisms. Since the early days of ethology, behaviors or components of a behavior have been used to infer phylogenetic relationships (Whitman, 1899; Lorenz, 1950; Tinbergen, 1959; Miller and Jearld, 1982; Miller and Robison, 1974; Mayr, 1958; Eberhard, 1982; Greene, 1977). The procedures for such research are usually grouped under the rubric "comparative method" (Hailman, 1976a), and are often held to be similar to the methods used by morphologists to study phylogenetic relationships. As outlined by Hinde and Tinbergen (1958), comparative analyses of behavior usually begin with the examination of several species and the recognition of behavioral similarities among the species. Then, either the patterns of behavioral similarity can be compared to a currently accepted phylogeny (Greene and Burghardt, 1978; also see Mayr, 1958) to see how sim-

ilar the pattern of relationships based on behavioral characters is to that based on morphological evidence, or the behavioral similarities themselves can be used to construct a phylogeny, as in the work of Lorenz (1941). Two important concerns have often been expressed by ethologists in relation to the process of using behavioral characters in phylogenetic analysis. The first is the problem of the units of behavior. What are the appropriate components of an organism's behavioral repertoire to use in a comparative analysis? Many workers have suggested that "fixed" action patterns be used in phylogenetic analysis because of their relative stereotypy and their consequent ease of identification (e.g., Bateson and Hinde, 1976). The second issue is the variability of behavior. If behavioral units appropriate for comparison cannot be reliably identified and if it is not possible to identify homologous similarities (an issue considered in detail below), then behavior would appear to have little value in historical analysis. This has led several investigators to conclude that behaviors have no utility whatsoever in the analysis of patterns of relationship (Aronson, 1981; Atz, 1970).

2. Ethological series. A second method used by ethologists to study the evolution of behavior is similar to the morphological series approach of morphologists (Lauder, 1981). If an investigator wishes to analyze the evolution of a complex behavior, for example, a comparative approach is taken in which taxa exhibiting similar but less complex behaviors are arranged in a series from the least complex to the most complex. This series is often taken as representative of a possible evolutionary pathway leading to the complex behavior, and interpretations of selection forces, behavioral transformations, and causative environmental factors are based on this series. A good example of this procedure is the analysis of Kessel (1955), who studied courtship behavior of balloon flies.

This approach has several pitfalls, not the least of which is the probable lack of congruence between a behavioral or morphological series and the pattern of transformation derived from a corroborated phylogenetic hypothesis of the relationships of the clade under study (Lauder, 1981). Behavioral or morphological series are artificial constructs of equilibrium points and are nonhistorical in nature.

3. Criteria for homology. The final and most important issue to consider in this examination of current approaches to historical patterns in ethology is the problem of recognizing behavioral homologies. Many criteria have been proposed by ethologists for determining which behaviors in a comparative analysis are homologous, and many workers have discussed extensively the value of these criteria. Virtually without exception, however, these discussions have had one premise: that homologous behaviors can be recognized by the application of criteria that are largely independent of phylogenetic patterns of character dis-

tribution. I term such criteria *a priori criteria for homology* because no reference is made to the phylogenetic distribution of other characters possessed by the clade. Three such *a priori* criteria have been of particular importance in ethology:

1. Two behaviors are homologous if the neural and neuromuscular control systems of the two behaviors are similar. I will refer to this as the *neural criterion*.
2. Two behaviors are homologous if the gross morphological features used in the behavior are homologous. I will refer to this as the *morphological criterion*.
3. Two behaviors are likely to be analogous if the biological role (function in ethological terminology) of the two behaviors is similar, and/or if the two behaviors could have been subjected to similar selection pressures. I refer to this as the *selection criterion*.

First, consider the neural criterion, which is perhaps the most commonly proposed *a priori* criterion for determining homologies. Baerends (1958, p. 409) has stated one version of this criterion clearly: "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." Other investigators have been equally impressed with the capability of the central nervous system of providing a reliable guide to behavioral homology, as the following quotations demonstrate:

Thus, uncovering a behavioral process which, in spite of superficial modifications, is shown to depend on homologous neural structures provides a valid criterion useful in a taxonomy of behavior—and valid criteria for classification are not abundant in the behavioral sciences. (Pribram 1958, p. 142).

The study of the evolution of the capacities to acquire new behaviors leads inevitably into the central nervous system as the locus of homologous structural correlates through which homologous behavioral capacities can be identified. (Hodos, 1976, p. 162).

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. (Hodos, 1976, p. 163).

Two concepts would appear to underlie application of the neural criterion: the idea that the central nervous system and the motor patterns it produces exhibit more conservative evolution than do behaviors, and the idea that there is a tight coupling between neural structure and behavior. In the absence of evidence supporting these ideas, it would be difficult to suggest that the nervous system is the map that

allows us to determine behavioral homologies. We need an explicit methodology for evaluating the linkage between neural and behavioral evolution.

There are several difficulties that arise with the application of the neural criterion, ignoring the fact that we know relatively little about the neural control of behavior, although the field of neuroethology is showing rapid progress (Hailman, 1976b). A simple theoretical example will introduce the discussion.

Consider the approach depicted in Figure 1-1. A clade of ten species is studied (A to I, with an outgroup species O) and a certain behavior is found to be present in five of these species (B, E, G, H, I, boxes in upper panel). This behavior is identical in these species. An analysis of the morphological and neural bases of this behavior reveals that species G, H, and I all show morphological and neural correlates of the behavior, but that species B and E possess only one correlate. Using an accepted cladogram (Figure 1-1, middle panel) as a basis, we can map the distributions of the behavioral, morphological, and neural novelties onto the cladogram to provide a basis for historical inferences about the evolution of behavior. In this case (Figure 1-1, lower panel), we see that the behavioral pattern shown by species B is not homologous with that of species E, and that the behavior is homologous within the monophyletic clade formed by species G, H, and I.

Figure 1-2 illustrates two possible outcomes of a theoretical study in the evolution of behavior relevant to our consideration of the neural criterion. Imagine that ten species of shrimp have been studied (A to I, with an outgroup species O) and that six species are found to display a particular escape behavior. High-speed films of this behavior demonstrate that the behavior is identical in all six species. The mapping of the occurrence of this behavior onto the cladogram (accepted as true on the basis of other characters) demonstrates that the behavior is homologous in species A, B, and C and in species G, H, and I, but not between these two groups. Thus, the behavior has evolved at least twice in this clade of shrimp.

Further neurobiological study reveals that in some species one neural circuit mediates this behavior, while in other species a completely different circuit composed of different motoneurons innervating different peripheral muscles controls the behavior. If the results of this study are as shown in the upper panel of Figure 1-2, then we may conclude that the independent evolution of similar escape behaviors in the two groups of shrimp was accompanied by the evolution of two different neural control systems for the behaviors. In this case, the patterns of variation in behavior and the neurobiology are historically congruent.

However, if the results of the study produce the pattern shown in the lower panel of Figure 1-2, then an entirely different conclusion may be drawn. In this case, a homologous behavior (the escape behavior in

TAXA FEATURES	A	B	C	D	E	F	G	H	I	O
MORPH	•		•		•		•	•	•	
NEURAL	○	○		○			○	○	○	
BEHAV		□			□		□	□	□	

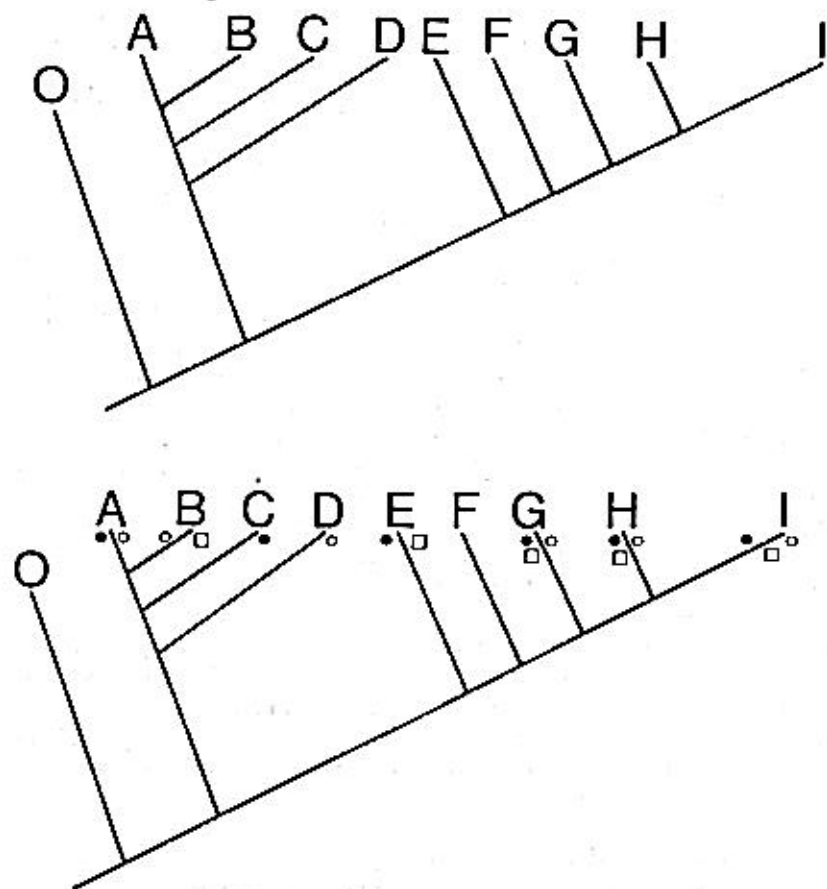
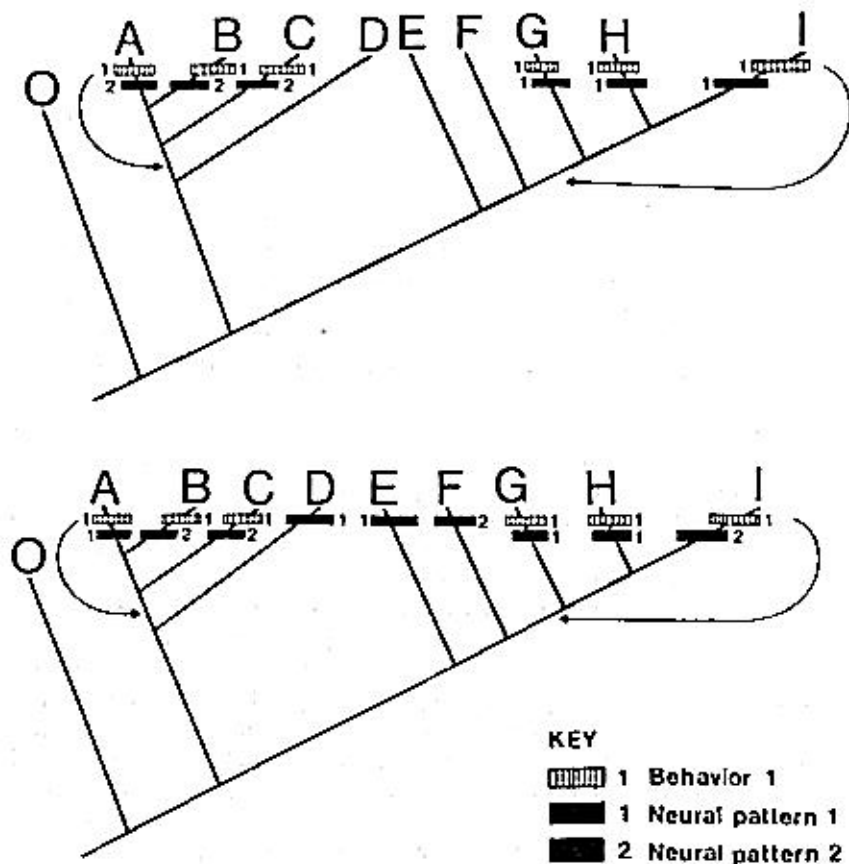


FIG. 1-1 A simple theoretical example to illustrate one procedure for studying the evolution of behavior and the neural and morphological bases of behavior. In this example, species A to I are studied (O is an outgroup clade) and several of the species are found to possess a particular behavior pattern indicated by the boxes in the upper panel. The behavior is identical in each of these species. Study of the morphological and neural patterns in these species shows that some species share a particular specialization indicated by the solid and open circles respectively. Using an accepted cladogram as a basis (middle



KEY
 □ 1 Behavior 1
 ○ 1 Neural pattern 1
 ○ 2 Neural pattern 2

FIG. 1-2 A simple theoretical example to illustrate application of the neural criterion for determining behavioral homologies. The two panels illustrate two types of mapping of behavioral and neural patterns we might expect if there is a tight historical coupling between neural and behavioral features (upper panel) and a loose coupling (lower panel). The distribution of two neural patterns is shown in relation to one behavior. Note that in both panels the behavior is homologous in taxa A, B, and C, as well as in taxa G, H, and I, but that the behavior is not primitive for the clade as a whole and thus is not homologous in these two groups. The cladogram is accepted as being correct; of course, the behavioral and neural characters could be used to modify the cladogram for subsequent analyses. Arrows indicate the level where the behaviors are inferred to have evolved. Also note that the distribution of characters on the lower panel shows that homologous behaviors may have nonhomologous neural substrates.

panel), the morphological, neural, and behavioral novelties may be mapped onto the cladogram (bottom panel). Inferences based on this pattern provide insight into the evolution of behavior.

species A and B) is mediated by nonhomologous neural systems. In addition, there is no clear relationship between the phylogenetic distribution of escape behavior and the type of neural circuit controlling the behavior. Here, the neural criterion fails.

The most important point is that the success or failure of the neural criterion depends entirely on the phylogenetic distribution of the neural components of a behavior in relationship to the phylogenetic distribution of the behavior itself. In some systems or types of behavior, there may be a tight coupling between neural and behavioral evolution, while in other cases there may be little relationship between behavioral and neural evolutionary novelties.

There are four specific reasons, grounded in recent findings in comparative neurobiology and neuroethology, why I believe that the neural criterion is not adequate as an indicator of behavioral homology. First, neural connections and structures can exhibit convergent evolution just like any morphological feature. There is no evidence to suggest an overall phylogenetic conservatism of neural connections or centers that could support use of the nervous system as an arbiter of behavioral homology. For example, Northcutt (1981) notes that pallio-spinal and cervical-spinal pathways apparently evolved independently in galeo-morph sharks, urodele amphibians, birds, and mammals. He summarizes one aspect of recent progress in neuroanatomy: "Perhaps we are discovering that active vertebrate predators have independently and repeatedly evolved complex and very similar nervous systems to solve a similar array of environmental problems." If features of nervous systems are just as likely to be convergent as behaviors or skeletal features are, then what basis is there to assign priority to neural information in determining homologies?

The second objection to the neural criterion stems from constraints on the design of neural circuits. To take one example, the types of possible circuits that produce patterned behavior are very few (four or five basic types). Each of the basic neural electrical circuits has a particular functional significance, and animals that produce patterned movements of a certain type tend to have those types of controlling circuits (see Bullock, 1961; Delcomyn, 1980). A similar argument has been made by Ulinski (1984) for constraints in the design of vertebrate sensory systems. In short, the range of possible engineering designs of pattern generators is limited, and convergence of neural control in unrelated animals that produce grossly similar patterned behaviors should be expected. Evidence of a similar neural circuit may have nothing to do with homologous behaviors because of the constraints on circuit design.

Thirdly, one neural circuit can mediate several different behaviors depending on the pattern of nerve impulses in the circuit. Are we to consider that all of the different behaviors controlled by a single circuit are homologous to one another because they have a common neural

basis? Croll and Davis (1981) provide an example of a situation in which a variety of motor programs are used to control the same motor system in *Pleurobranchia*, and similar findings were obtained by Ayers and Davis (1977) and Ayers and Clarac (1978) in their studies of lobster (*Homarus*) walking. Similar neural circuits and similar peripheral morphologies (arrangements of muscles and bones) are no guarantee that the behaviors produced by these systems will be similar. The converse of this third objection to the neural criterion also holds: very similar behaviors can be elicited by different patterns of neural stimulation. A conclusion of Hoyle's (1976) research on the neurophysiology of insect locomotion, in which the pattern of motor output to locomotor muscles during normal locomotion was very variable, was that "widely different patterns underlie even quite similar movements."

The fourth and final objection to the neural criterion is that homologous neural circuits can mediate different behaviors because of changes in the peripheral morphology. If muscles change their origins and insertions in one group of species and the neuromuscular output to those muscles remains the same as in other species in the clade, then the patterned movements produced by the bones will be different in the clade with the new muscle arrangement, even though the neural substrate may be homologous. An example of this can be found in the body movements of decapods used in locomotion. Paul (1981a, 1981b) proposed homologies between the motoneurons, muscles, and motor output to the muscles in the tails of two unrelated decapod families. Yet the movements produced by these homologous systems are very different in the two families.

These four arguments based on comparative neurobiology have been adduced to demonstrate that there is little support for the neural criterion in the literature of neurobiology. Furthermore, the simple example of Figure 1-2 illustrates that a phylogenetic approach (discussed in more detail in the next section below) indicates that behaviors may be homologous even though the neural substrates are not. There is no reason to presume a one-to-one mapping between the nervous system and behavior; each is capable of divergent evolutionary patterns.

The second a priori criterion for determining behavioral homologies mentioned above is the morphological criterion. This is similar to the neural criterion in that both rely on an underlying structural substrate to a behavior as the arbiter of homology. This criterion is perhaps the most widely cited, and the following quotations give a sample of ethological opinion on this issue:

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. (Atr, 1970, p. 68).

It is manifestly impossible for nonhomologous structures to have homologous functions. (Aiz, 1970, p. 60).

Behavioral homology has been defined here in the context of specific structural entities that are homologous. . . . Behaviors associated with . . . two homologous structures would therefore be homologous no matter how different the function of the two behaviors were (Hodos, 1976, pp. 160-161).

The concept of behavioral homology is totally dependent on the concept of structural homology. . . . If evidence comes to light indicating that structures previously thought to be homologous are not homologous, then any behaviors associated with these structures must also be redesignated non-homologous (Hodos, 1976, p. 165).

Functions, considered as abstractions and without consideration for the structures that perform these functions, should not be spoken of as homologous. (Haas and Simpson, 1946, p. 323).

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).

The morphological criterion may be subjected to a similar analytical procedure to that used for the neural criterion (Figures 1-1 and 1-2). Mapping behavioral and morphological (structural) novelties onto a cladogram will allow us to determine if there is a tight historical linkage between the two. If, as in Figure 1-1, homologous behaviors can have nonhomologous morphological substrates, then the morphological criterion will be of little value in determining behavioral homology. Because there is so little data bearing on the problem of congruence between morphological and behavioral novelties, excessive reliance on morphology as an arbiter of behavioral homology may lead to erroneous conclusions.

An important consideration in an analysis of the morphological criterion is the problem of the homology of functions (use of structures). Under what circumstances can functions be considered to be homologous? Haas and Simpson (quoted above) felt that unless there was a definable morphological substrate, functions could not be homologous. If we choose to identify convergences by relying on a criterion of similar functions (as "the wing of a bat and the wing of an insect are convergent because they have similar functions but different structures") then it will be difficult to recognize homologous functions. I suggest that functions can be homologous, can be used as systematic characters, and can be recognized as such on the basis of their phylogenetic distribution (examples will be given in the case study).

One example of the confusion that can result from the application

of the morphological criterion to the homology of functions is found in the following statement: "The insertion of food into the mouth by a man and a monkey would be both homologous (because the hands of monkeys and humans are derived from hands of their common ancestors) and analogous (because the behaviors serve the same purpose)" (Hodos, 1976, p. 160). One might question the utility of a criterion that leads to the determination of a behavior as both homologous and convergent.

The third a priori criterion for the recognition of behavioral homologies is the likelihood that the behaviors under consideration could be subject to selection and thus could be convergent. This criterion relies on the argument that behaviors that are subject to strong selective forces are more likely to be convergent.

Illustrative remarks in support of the selection criterion follow:

A knowledge of the selective factors exerting pressure on the animal will, therefore, help to judge how far in a certain case the possibility of convergence has to be taken into consideration (Baerends, 1958, p. 409).

Behavior is subject to particularly strong selection. . . . Strong selection pressures, especially those associated with rigorous environments, tend to result in convergences (Aiz, 1970, p. 64).

Parallelisms and analogies are particularly common in all types of behavior that are strictly functional, such as food getting or locomotion (Mayr, 1958, p. 351).

The selection criterion may be criticized by noting the difficulty of demonstrating that any feature is under selection pressure. Indeed this criterion assumes *directional* selection, and that the selection pressures on behaviors in the present habitat were those that shaped the behaviors in the past. Cracraft (1981) has criticized morphologists for their axiomatic acceptance of concepts of selection and their failure to undertake research programs that *test* the role of selection in producing morphological patterns. The same criticism can be applied to the selection criterion of homology recognition: the use of selection is axiomatic, not deductive. There is to my knowledge no way to determine selection pressures (magnitude and direction) and their effect on behavior by simply examining the behavior of a few individuals. Knowledge of intrapopulation variability in relation to fitness is necessary (Lande and Arnold, 1983), and a detailed, specific research program for studying selection has been outlined by Arnold and Wade (1984a, 1984b). I conclude that the axiomatic application of the selection criterion is unlikely to contribute to decisions about the likelihood of homology and convergence of behavior, and that broad statements about the significance of selection for the study of behavior only mask our ignorance about the nature of variation in behavior, its genetic basis, and its relation to fitness.

HISTORICAL ETHOLOGY

Since the early 1970s, morphologists and systematists have made major advances in our understanding of research methodologies and concepts in comparative and historical biology. Unfortunately, ethologists have generally not been aware of this progress, and as a result most recent discussions of homology and convergence have not utilized recent terminology or benefited from modern conceptual clarifications. The approach taken here will be similar to that of recent discussions of homology by comparative biologists (see Eldredge and Cracraft, 1980; Wiley, 1981; Cracraft, 1981; Nelson, 1970; Patterson, 1980, 1982). My aim is to illustrate the conceptual basis of one approach to historical ethology: the comparative phylogenetic approach. This theoretical discussion will serve as the basis for the specific example discussed in the case study below.

A simplified scheme for phylogenetic analysis may be outlined as follows. First, some preliminary decision must be made about which taxa are to be included in the study and the limits of those taxa. Next, similarities among the taxa are recognized. These similarities are provisional hypotheses of homology (Cracraft, 1981). Third, the similarities are clustered into nested sets defining a hierarchy of taxa. In general the clustering procedure uses a set of working rules that minimizes the number of steps used to produce the hierarchy. For analyses with many taxa and many similarities (characters), computer programs are available that produce one or more branching diagrams based on a variety of different assumptions. Such a hierarchy can be expressed as a branching diagram (e.g., Figures 1-1 and 1-2). Invariably, some of the proposed similarities from the second step are found to indicate a relationship between two taxa that is in conflict with the relationships indicated by other similarities. Those conflicting characters are *convergences*, as they are in conflict with the hierarchical pattern corroborated by the majority of other characters. As Patterson (1980, p. 236) notes, "In other words, these characters fail the principal test of homology, congruence with other characters."

The character conflicts in the branching diagram could have been produced by a variety of processes such as learning, convergent evolution, mimicry, and chance. Additional research would be needed to evaluate explanations for each character conflict. Such additional investigation of specific characters is often undertaken if no clear branching diagram emerges from the clustering of characters into nested sets. Thus, if an attempt to generate a corroborated branching diagram results in as many (or more) characters conflicting with the diagram as supporting it, then individual character conflicts may be investigated in an attempt to better resolve the pattern of character distribution.

The most widely discussed source of additional information on char-

acters is ontogeny. The pattern of development may provide data that resolve conflicts in the branching diagram by demonstrating that two characters initially thought to be similar (and thus providing evidence of relationship between two species) are in fact different.

Key results of this method of phylogenetic analysis are that *homologous similarities are those that define monophyletic (natural) groups* (Patterson, 1982), and that we recognize similarities as homologies only as a *consequence* of examining the distribution of other characters. Thus, homologies are recognized a posteriori, and are a consequence of accepting a particular phylogeny as being an accurate depiction of the pattern of ancestry and descent. To use the example from Figure 1-2, it is unparsimonious to assume that the escape behavior is homologous between species C and G, as this would imply that taxa D to F had lost this feature. If we accept the evidence from other characters that the branching diagram shown in Figure 1-2 is the corroborated hypothesis of phylogenetic relationship, then escape behavior has evolved twice. Thus, as discussed by Patterson (1982), homologies characterize natural groups and such groups are individuals in the sense of Hull (1978) and Ghiselin (1974); individuals are coherent spatiotemporal entities that participate in natural processes (Wiley, 1981). Analogies, on the other hand, characterize *classes* (Ghiselin, 1984) of taxa, groupings that do not participate in natural processes and are spatiotemporally unrestricted. Paraphyletic and polyphyletic groups are classes. Ethologists unfamiliar with these concepts in phylogenetic analysis are referred to the general texts by Wiley (1981) and Eldredge and Cracraft (1980), and the excellent discussions of homology in Patterson (1980, 1982).

To take one final example from the field of comparative neuroethology, consider the distribution of species of fishes that can use electroreception to obtain information from the environment. Electroreception appears to be a sensory modality that is primitive for vertebrates (Bullock et al., 1983). However, within the teleost fishes (which primitively lack an electric sense), electroreception has reevolved several times. Even though the mormyrid fishes and the gymnotid fishes both possess similar types of ampullary receptors, have afferents that enter the brain through the anterior lateral line nerve, and have similar specializations of the medial nucleus, the evidence for convergent evolution of this sensory modality is convincing because of the large number of other similarities that corroborate a phylogenetic hypothesis different from one based on the concept that the electroreceptive systems are homologous.

While this may seem a trivial and obvious point, the implications of the congruence criterion for homology recognition have not been appreciated by ethologists, nor, for the most part, have the implications been incorporated into comparative ethological research programs. Some investigators have defended the view that methods and procedures of phylogenetic analysis are not applicable to the study of behav-

ior: "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)," and "one should be aware of the pitfalls in trying to build phylogenetic trees of behavior or to establish behavioral homologies across large phyletic gaps by using morphological methods" (Aronson, 1981, p. 37). Atz (1970) has expressed similar reservations based on the difficulty of recognizing behavioral homologies by a priori criteria.

If the primary test of homology is congruence with other characters, then there is no reason to assume prior to a phylogenetic analysis that one particular class of characters (such as behaviors) will not be useful indicators of phylogeny and will be expected to show a great deal of convergence. Furthermore, there is no reason to rule out the analysis of functions (uses of structures) as possible characters for understanding transformations of biological designs and behaviors. To my knowledge, no study has considered patterns of distribution of function, behavior, and morphology within a historical context, and no attempt has been made to explicitly define the transformational relationship among these three types of biological features. We will never know if behaviors or functions are too variable or have low utility for studying evolutionary transformations unless research programs explicitly address the question of historical congruence among behaviors, functions, and morphological patterns in an attempt to identify general features of biological transformations.

A CASE STUDY IN THE EVOLUTION OF BEHAVIOR

Goals and Research Approach

The purpose of presenting this case study is to provide a detailed example of a phylogenetic and historical approach to the analysis of behavioral, morphological, and functional patterns. The approach taken will be a posteriori in that homologous characters will be identified on the basis of their congruence with a phylogenetic hypothesis. This case study addresses a general problem in ethology: the relationship among the transformation of form, function, and behavior.

The subject of the case study is the feeding behavior of sunfishes (family Centrarchidae), an endemic North American family of 32 species. Within this family two species exhibit a derived feeding behavior and eat snails; the snails are crushed in the pharyngeal area of the mouth before being swallowed. Most other sunfish species have a relatively diverse diet (Keast, 1978a, 1978b; Savitz, 1981). The two species that do eat snails, the pumpkinseed sunfish (*Lepomis gibbosus*) and the redear (*L. microlophus*), have specialized feeding behavior in that the

snail shells are crushed in the pharynx and then the shell is separated from the body and ejected from the mouth before the body itself is swallowed (Lauder, 1983a, 1983b). The snail is not swallowed whole.

An analysis of the evolution of this snail-crushing behavior is particularly suitable for addressing the general questions raised above because (1) the behavior is specialized and is not widespread within the family, (2) there are morphological specializations in the feeding mechanism of species that regularly exhibit the crushing behavior, (3) the physiological basis of the crushing behavior can be studied experimentally by recording electrical activity from the muscles that are involved in crushing the snails (thus the motor patterns used in the behavior can be identified), and (4) the crushing behavior has previously been identified as being composed of repetitive crushing phases (Lauder, 1983b). As Selverston (1976, p. 82) asserts, "If we are to understand how nervous systems generate behavioral activities, cyclically repeating motor patterns are a good place to start. By their very nature, they allow repeated study of the basic mechanisms involved." Other authors have emphasized the importance of studying the underlying physiological and motor bases of behaviors (e.g., the papers in Fentress, 1976, by Bullock, Kennedy, and Hoyle; Barlow, 1977; Greene and Burghardt, 1978; Delcomyn, 1980), but few studies are available in which such comparative physiological patterns are available for taxa in which concomitant behavioral, morphological, and phylogenetic analyses have been conducted.

In this case study, a particular phylogenetic hypothesis is taken as a starting point from which to consider the patterns of behavioral, morphological, and physiological features. This phylogenetic hypothesis, derived from work currently in progress, indicates the corroborated relationships of some of the centrarchid species, and does *not* rely on characters discussed here for evidence supporting the phylogeny. Thus, the characters that are discussed in this paper were not used to make the phylogeny initially. Given this pattern of genealogical relationship as a starting point, the characters of interest in this analysis are compared to the phylogeny. Snail-crushing behavior, morphological specializations in the feeding mechanism, and motor patterns are all mapped onto the phylogeny to determine if patterns of evolution in these characters are congruent. This procedure allows us to assess the neural and morphological criteria for homology. The neural criterion would be corroborated, for example, if the phylogenetic distribution of the motor patterns producing the snail-crushing behavior was congruent with the phylogenetic distribution of the behavior itself.

Materials and Methods

Individuals of all genera in the family Centrarchidae were studied morphologically, and most species within the largest genus, *Lepomis*, have

also been examined. Dissections of the head were used to ascertain the basic design of the feeding mechanism. Muscle orientations were examined in most species to determine the range of variation in the clade, and muscle size was studied by measuring the physiological cross-section of the muscles in the pharynx. Physiological cross-sections (Gans and Boek, 1965) provide a relative measure of the force a muscle is capable of generating, and this measure takes into account differences between muscles in fiber arrangement and length. Details of the measurements and techniques may be found in Lauder (1983b). The size of teeth on the pharyngeal bones was quantified by digitizing the areas of teeth on the pharyngeal jaws of nine species.

Information on the trophic biology of sunfish species was obtained from the literature and from laboratory observations. Only two species, *Lepomis gibbosus* and *L. microlophus*, would regularly eat snails in the laboratory, and these two species also are the chief natural molluscivores within the Centrarchidae (Savitz, 1981; Gosline, 1985). Individuals of one other species of centrarchid, *Lepomis cyanellus* (green sunfishes), would eat snails in the laboratory. Other species such as the bass (*Micropterus*) or the bluegill sunfish (*Lepomis macrochirus*) refused to eat snails.

In order to determine the motor patterns involved in feeding behavior, electrical recordings were made from the pharyngeal muscles in unrestrained, active fishes. Electromyograms were recorded using fine-wire bipolar electrodes implanted percutaneously into pharyngeal muscles in anesthetized fish. When the fishes recovered from anesthesia, the electrode leads (see Lauder, 1983b, for details) were attached to Grass P511J amplifiers and signals were recorded on FM tape for subsequent analysis. Nine species in the Centrarchidae have been studied experimentally to date: *Ambloplites rupestris*, *Pomoxis annularis*, *P. nigromaculatus*, *Micropterus salmoides*, *Lepomis cyanellus*, *L. gulosus*, *L. macrochirus*, *L. gibbosus*, and *L. microlophus*. In addition, electromyographic recordings were made from hybrids between *L. microlophus* and *L. cyanellus*. Three types of food were used: pieces of earthworm (*Lumbricus*, 1 to 8 cm long), snails (*Helisoma*, 2 mm to 1 cm in diameter), and small minnows (*Pimephales*, 3 to 6 cm total length).

Results

Figure 1-3 shows a schematic view of the feeding apparatus of a centrarchid fish. The oral jaw apparatus is located at the front of the buccal cavity (BC, OJA) and is used during initial prey acquisition by the suction feeding mechanism characteristic of teleost fishes (Lauder, 1982). Once the prey has been captured and is located in the buccal cavity, water flow through the mouth is used to move the prey posteriorly to the pharyngeal jaw apparatus (PJA). The pharyngeal jaw bones are used to move prey into the esophagus (ES) and to manipulate prey prior to swallowing. Figure 1-3 shows the position of a snail between the upper

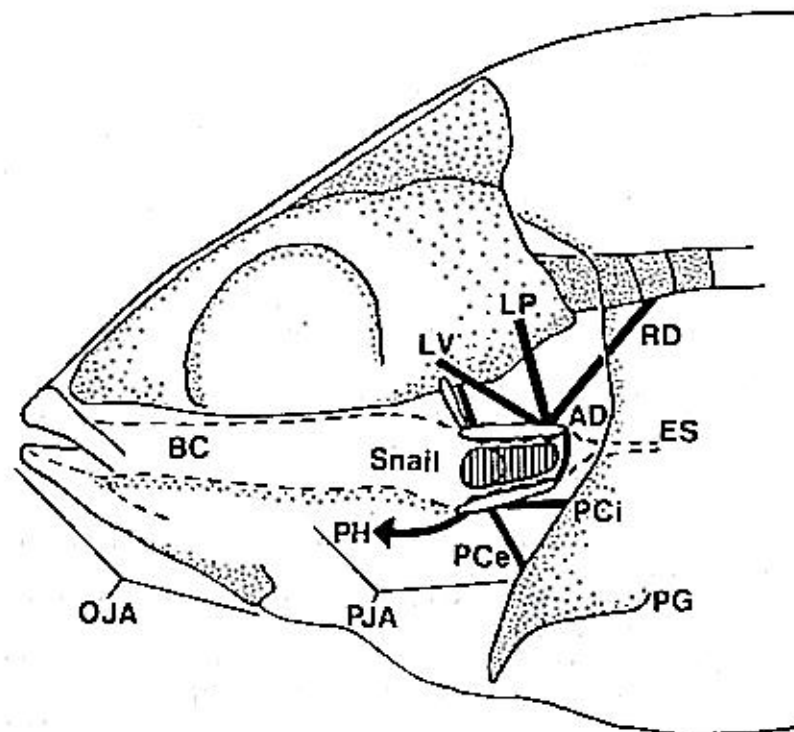


FIG. 1-3 Schematic view of the head of a centrarchid sunfish to show the location of the major morphological units associated with feeding behavior. Fishes possess two major sets of jaws: an oral jaw apparatus (OJA) and a pharyngeal jaw apparatus (PJA). A snail is shown between the pharyngeal jaws in the position used by the fish for crushing. Abbreviations: AD, fifth branchial adductor muscle; BC, buccal cavity; ES, outline of the esophagus; LP, levator posterior muscle; LV, external and internal branchial levator muscles; OJA, oral jaw apparatus; PGe, pharyngocleithralis externus muscle; PGi, pharyngocleithralis internus muscle; PG, pectoral girdle; PH, pharyngohyoideus muscle; PJA, pharyngeal jaw apparatus; RD, retractor dorsalis muscle.

and lower pharyngeal jaw bones when the shell is being crushed (as determined by x-ray cinematography, Lauder, 1983b). The upper and lower pharyngeal jaws are connected by a short muscle, the fifth branchial adductor (AD). Many other muscles (some of which are shown in Figure 1-3) attach the pharyngeal jaws to the skull and surrounding bony elements such as the pectoral girdle (PG). This basic musculo-skeletal design is common to all centrarchid fishes and does not vary within the species studied. Snail-eating sunfishes thus possess the same basic design as other trophic types in the family, and no new muscles, bones, or muscle origins or insertions are present.

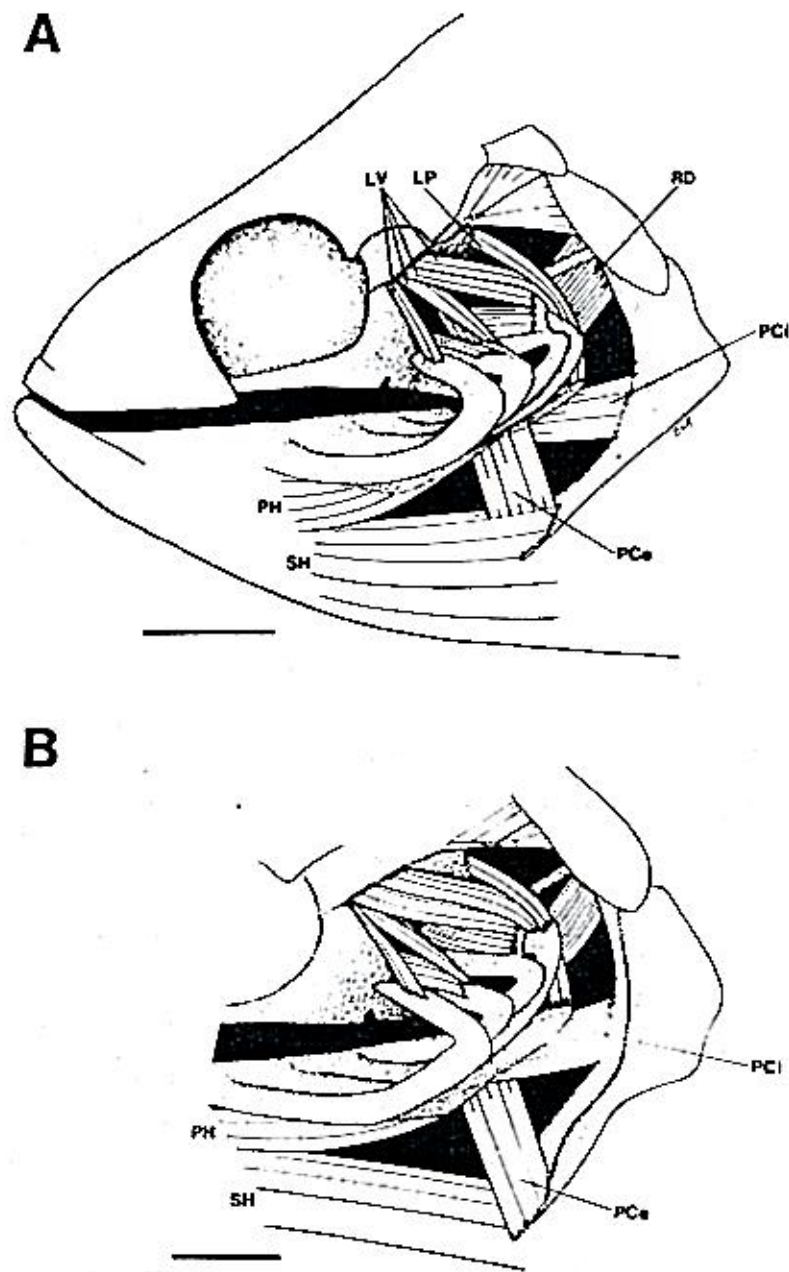


FIG. 1-4 Lateral view of the pharyngeal apparatus in (A) *Lepomis gulosus* and (B) *Acantharchus pomotis* to illustrate the anatomical organization of this region. Comparative illustrations of other centrarchid fishes are presented in Lauder (1983b). Scale = 5 mm. Abbreviations: SH, sternohyoideus muscle; others follow those in Figure 1-3.

The musculature of the pharyngeal region is shown in more detail for two species in Figure 1-4. The upper pharyngeal jaw on each side is attached to the skull by a series of branchial levator muscles (LV) and to the vertebral column posteriorly by the retractor dorsalis muscle (RD). Ventrally, the lower pharyngeal jaw on each side is attached to the pectoral girdle by the pharyngocleithralis internus and externus muscles, and to the hyoid anteriorly by the pharyngohyoideus (PCI, PCe, PH).

Examination of the physiological cross-sections of the pharyngeal muscles in four species (Table 1-1) shows that the two snail-eating species share two characters: hypertrophy of the pharyngohyoideus (PH) and levator posterior (LP) muscles. None of the other muscles in the pharynx of these two species is significantly enlarged relative to pharyngeal muscles in other species.

The pharyngeal jaw bones of several representative species of centrarchids are illustrated in Figure 1-5. The lower pharyngeal jaw is composed of a pair of bones that attach anteriorly via ligaments to the branchial apparatus. The upper pharyngeal jaws consist of several bones (pharyngobranchials and epibranchials) that are closely articulated with each other and bear enlarged toothplates. *Lepomis microlophus* and *L. gibbosus* have robust lower pharyngeal jaws in comparison to the other species, and have larger and more rounded teeth (Figure 1-5; Table 1-2). In both of these species, the upper pharyngeal jaw teeth are hypertrophied with respect to the lower jaw teeth (Table 1-2).

Two basic types of motor patterns in the pharyngeal muscles were discerned in the species studied electromyographically. First, during the swallowing of fishes and worms, all species except one (the redear, *L. microlophus*) display a rhythmic pattern of muscle activity that may continue for up to a minute as the prey is moved from the pharyngeal area into the esophagus. Examples of this rhythmic swallowing pattern are shown in Figure 1-6; more quantitative representations of this sequence of muscle activity are given elsewhere (Lauder, 1983b). Note that there is a considerable difference between the activity patterns of different pharyngeal muscles (e.g., the PCe and PCI in Figure 1-6B).

TABLE 1-1 Branchial muscle physiological cross-sections (mm^2) in centrarchid sunfishes. Data are given for eight muscles in four species. See text for discussion. Muscle abbreviations: AD5, fifth branchial adductor; LE1, levator externus one; LE3/4, levatores externi three and four; LP, levator posterior; PCe and PCI, pharyngocleithralis internus and externus; PH, pharyngohyoideus; RD, retractor dorsalis.

	RD	AD5	PH	PCI	PCe	LE1	LE3/4	LP
<i>Lepomis macrochirus</i>	5.2	1.8	2.0	3.5	5.8	1.0	2.8	1.0
<i>L. cyanellus</i>	9.3	4.1	1.9	3.5	4.3	0.9	3.4	1.7
<i>L. microlophus</i>	3.2	3.5	7.3	5.1	5.5	1.2	3.9	16.7
<i>L. gibbosus</i>	6.9	6.3	6.7	6.7	10.7	2.1	3.6	11.3

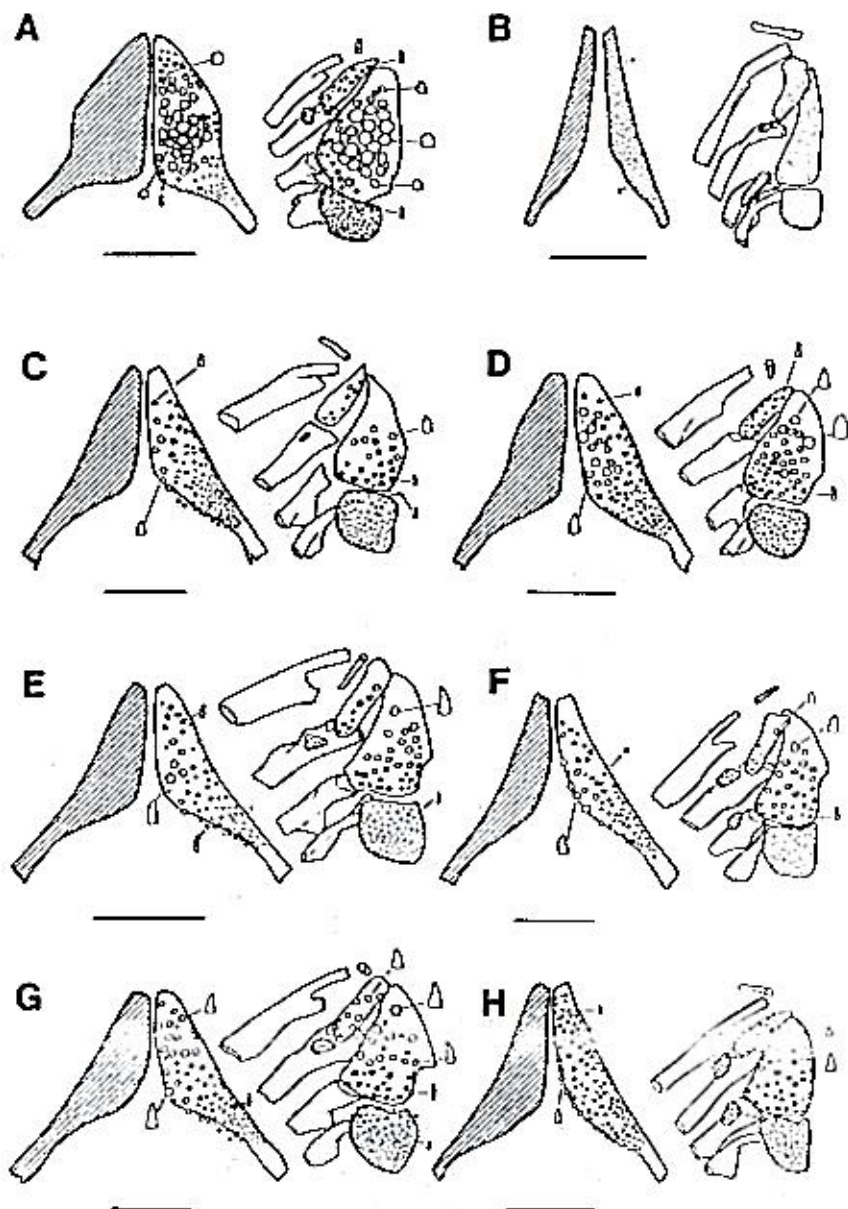


FIG. 1-5 Dorsal views of the lower pharyngeal jaws (on the left in each panel, with the left jaw shaded to emphasize shape differences), and a ventral view of the upper pharyngeal elements of the right side of the head (on the right in each panel). Representative teeth are shown in side view. Note the differences between the structure of the pharyngeal jaws in *Lepomis microlophus* and *L. gibbosus* in comparison to the other species. A, *Lepomis microlophus*; B, *Pomoxis nigromaculatus*; C, *L. punctatus*; D, *L. gibbosus*; E, *L. auritus*; F, *L. cyanellus*; G, *L. megalotis*; H, *Ambloplites rupestris*.

TABLE 1-2 Pharyngeal tooth areas in sunfishes (mm²) on the upper pharyngeal jaws (UPJ) and lower pharyngeal jaws (LPJ).

	UPJ	LPJ
<i>Ambloplites rupestris</i>	0.008	0.006
<i>Lepomis auritus</i>	0.012	0.016
<i>L. megalotis</i>	0.028	0.021
<i>L. microlophus</i>	0.066	0.046
<i>L. punctatus</i>	0.013	0.015
<i>L. cyanellus</i>	0.017	0.013
<i>L. gibbosus</i>	0.071	0.029
<i>L. macrochirus</i>	0.011	0.014
<i>L. gulosus</i>	0.009	0.004

and that the muscle activity shown represents only a small portion of a much longer duration sequence of this rhythmic activity.

The second basic type of motor pattern was observed when snail shells were crushed between the pharyngeal jaws. During snail crushing, nearly all pharyngeal muscles were electrically active simultaneously, and no rhythmic alternating pattern was observed (Figure 1-7B and C). In some experiments a hydrophone was placed in the aquarium to determine when in the course of muscle activity the snail shell cracked (see Figure 1-7B). The first sign of shell failure invariably occurred at the end of the burst of muscle activity as illustrated in the bottom trace of Figure 1-7B, and successive bursts of muscle activity produced less sound until the shell was completely crushed. After being crushed, the shell is separated from the snail by a different motor pattern from that used in crushing, and the shell fragments are ejected from the mouth cavity. The snail is then swallowed.

Statistical analyses reveal that the motor pattern used in snail crushing is less variable than that used in swallowing fish or worms (Lauder, 1983b). Muscle activity bursts are shorter and pharyngeal muscles are more similar to each other in the crushing motor pattern than in the swallowing pattern used for fish and worms. One striking result of this comparative analysis of the motor patterns used in processing food in the pharynx is that one species (*Lepomis microlophus*) uses the crushing pattern for all types of prey, even fish and worms (Lauder, 1983a). The other species that eat snails (*L. gibbosus* and *L. cyanellus*) use the crushing motor pattern when feeding on snails, but use the rhythmic swallowing pattern when feeding on fish and worms (compare A and C in Figure 1-7). These species, in contrast to *L. microlophus*, modulate the motor pattern to the pharyngeal muscles depending on the type of prey they are processing. On the other hand, the redear sunfish uses the same basic motor pattern for all prey.

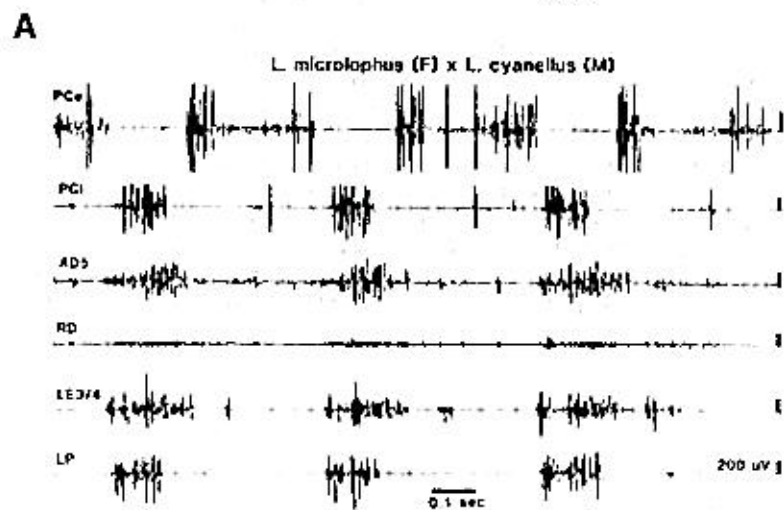


FIG. 1-6 Representative electromyographic recordings from pharyngeal muscles in (A) *Lepomis gulosus* and (B) a hybrid between *L. microlophus* and *L. cyanelus*. These data were obtained during swallowing of an earthworm (5 to 7 cm in length). All muscles in each panel were recorded simultaneously.

Discussion

Figure 1-8 summarizes the distribution of characters derived from the motor patterns in the pharyngeal muscles (black bars), morphological specializations in the pharynx (stippled bars), behavioral specializations (bars with vertical hatching), and ecological specializations (cross-hatched bars). The branching diagram depicting the relationships among the sunfish species is derived from other characters and is not fully resolvable with current information (note the four trichotomies). On the basis of this branching diagram, *Lepomis gibbosus* and *L. micro-*

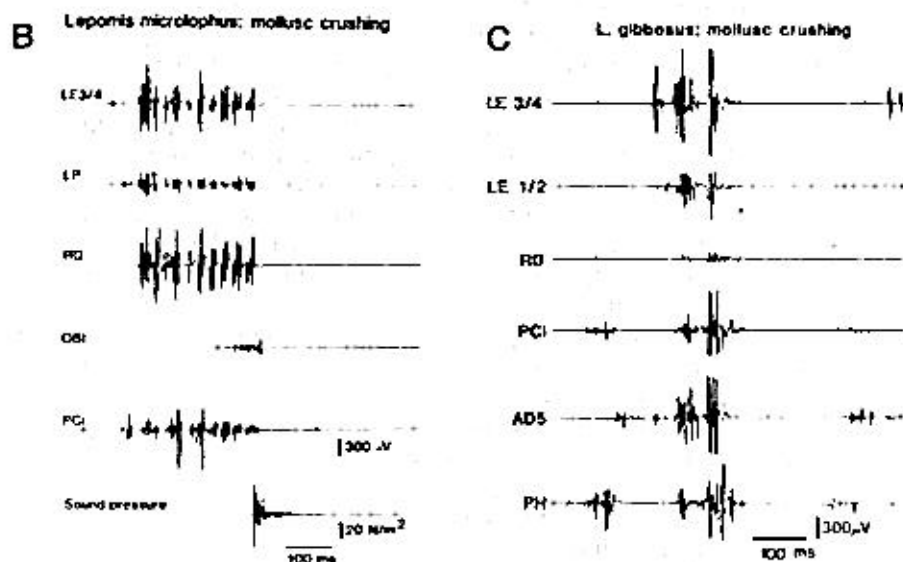
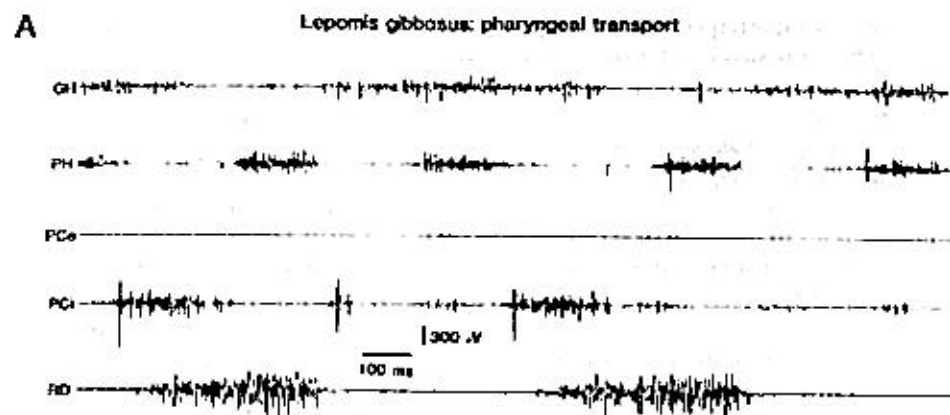


FIG. 1-7 Electromyographic recordings of pharyngeal muscles in *L. gibbosus* and *L. microlophus* during feeding on a worm (A) and on snails (B and C). Note the difference between the motor patterns in *L. gibbosus* in A and C. Snail-crushing patterns exhibit extensive overlap between pharyngeal muscles, in contrast to the rhythmic alternating pattern used for fish and worms, *L. microlophus*, however, uses the crushing pattern for all prey types (from Lauder, 1983a).

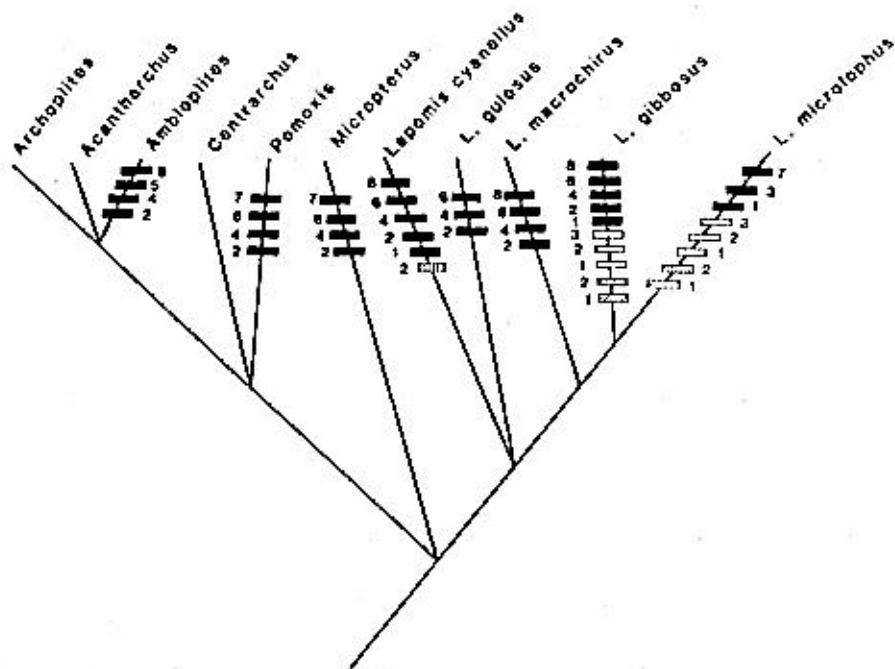


FIG. 1-8 Branching diagram depicting the phylogenetic relationships between selected centrarchid species (from Lauder, in preparation). Characters on the diagram are those resulting from the study of feeding behavior, morphology, and physiology, and were not used to generate the initial branching diagram. Bars are coded to indicate different types of characters. *Ecological features* (cross-hatched bars): 1, snails form a prominent component of the diet. *Behavioral features* (vertically hatched bars): 2, crushing behavior during feeding on snails. *Morphological features* (stippled bars): 1, hypertrophy of the pharyngohyoideus muscle; 2, hypertrophy of the levator posterior muscle; 3, expanded tooth areas on the upper and lower pharyngeal jaws. *Functional features* (black bars): 1, crushing motor pattern with extensive coactivation of pharyngeal muscles; 2, the retractor dorsalis and levator internus muscles alternate in activity during pharyngeal transport; 3, loss of rhythmic alternating motor pattern; 4, pharyngocleithralis internus has one burst of activity overlapping activity in the retractor dorsalis muscle; 5, pharyngocleithralis externus muscle has only one burst of activity, between adjacent bursts of the retractor dorsalis; 6, pharyngocleithralis externus muscle has two or three bursts, with extensive overlap in activity with the retractor dorsalis muscle; 7, pharyngohyoideus muscle has a double burst pattern with each burst overlapping activity in the retractor dorsalis; 8, triple burst pattern in the pharyngohyoideus muscle; 9, pharyngohyoideus muscle displays one burst of activity per swallowing cycle, alternating activity with the retractor dorsalis.

lophus are hypothesized to be sister groups (each other's closest relatives), and the other three *Lepomis* species on the diagram are proposed to be outgroups to this pair. Again, note that the numbered bars in Figure 1-8 are not used to support the branching diagram; they represent the distribution of characters derived from the case study on a previously corroborated phylogeny.

From this figure, we can consider that functional (black bar) characters 2, 4, and 6 are primitive for the clade, as they occur in all species except *L. microlophus* (*Ambloplites* lacks character 6). Thus, the phylogenetic distribution of these aspects of the motor pattern indicates that they represent a primitive component of the feeding behavior in this clade and that these characters are homologous in all taxa in which they are found. Other aspects of the motor pattern are specialized in some species. For example, *Ambloplites* has two unique features (numbers 9 and 5, black bars) that are not found in any other species. Functional character 7, occurring in *Pomoxis*, *Micropterus*, and *L. microlophus*, is, by itself, indicative of shared ancestry among these three taxa. However, this interpretation conflicts with the corroborated branching diagram and thus feature 7 must be convergent in at least one of the three taxa that possess it. The major specialization of motor patterns occurs in *L. microlophus* (character 3, black bar). This species has lost the rhythmic alternating motor pattern and uses the crushing pattern for all prey. The distribution of functional characters that relate to the rhythmic swallowing pattern indicates that possession of this pattern is primitive for the clade and homologous within it.

Within this clade, only two species have a prominent molluscan component to their diet, and the distribution of this ecological feature on the cladogram (character 1, cross-hatched bar) is congruent with the sister-species relationship of the pumpkinseed and redear sunfish. Also congruent with this branching pattern is the distribution of the three morphological specializations (characters 1, 2, 3, stippled bars). The most parsimonious interpretation of this congruent pattern is that a series of morphological, ecological, and behavioral novelties were acquired after the speciation event that gave rise to *L. macrochirus* and before or at the speciation event splitting the redear and pumpkinseed sunfish.

The final feature of interest is the crushing motor pattern in the pharyngeal muscles (character 2, vertically hatched bars). This motor pattern occurs in three species: *Lepomis microlophus*, *L. gibbosus*, and *L. cyanellus*. This motor pattern is homologous in the two snail-crushing species because it is congruent with the branching diagram, but it appears to be convergent in the green sunfish, *L. cyanellus*. Further information on the phylogenetic position of other *Lepomis* species and a resolution of the unresolved areas of the phylogeny are necessary to demonstrate that the green sunfish convergently possesses this character. However, it is clear from the distribution of this character in Fig-

ure 1-8 that the homology of this motor pattern within the clade is in doubt and that resolution of the issue depends on further phylogenetic analysis.

CONCLUSIONS

One major conclusion from this case study is that the distribution of functional, morphological, and behavioral features of a character complex are not necessarily congruent with each other. The implication is that each type of character is subject to convergence, and even complex motor patterns may be independently derived. From this example, it would appear that the neural criterion has little utility as an arbiter of behavioral homology. Within the sunfishes, morphological design in the pharyngeal region has remained conservative with no major alterations in pattern, and yet motor patterns controlling the pharyngeal muscles have changed greatly. Homologous muscles and other morphological elements have not retained their primitive pattern of activation and movement. The redear sunfish has completely lost the primitive motor pattern of rhythmic alternating activity, and although this species retains the primitive musculoskeletal design of other species in the Centrarchidae, a new motor pattern occurs that is unique to this species. No other teleost fish studied to date possesses such a novel motor pattern that is used for all prey. In this case, the peripheral morphology associated with the behavior appears to have remained relatively conservative, while the neural control has been modified considerably.

A second important point to emerge from this case study is that in the absence of functional information, a different interpretation might have been placed on the patterns. Yet, data on motor patterns are precisely what is lacking in so many comparative ethological investigations. In this case study, the major specializations and convergences within the clade were functional, and I think it highly unlikely that it would have been possible to predict a priori the distribution of motor programs within the clade based on morphology and behavior of the species. The data emphasize the extent to which transformations of motor patterns are involved in the evolution of behavioral specialization, and that "similar" behaviors may be mediated by very different motor programs.

In this chapter I have attempted to provide an analysis of a common (but not the exclusive) approach of ethologists to the analysis of homology. I have emphasized a priori avenues of ethological investigation because of the importance that these are usually accorded in general discussions and in research programs. I believe that arguments for homology in the absence of a direct link to a phylogenetic hypothesis are weak, and that the strongest test of homology is congruence with

other characters. The phylogenetic approach has the added merit of providing a method of testing the assumptions about relative constancy of neural and morphological systems assumed by a priori arguments. An important future task of comparative ethologists must be to acquire more examples of phylogenetic patterns of behavior in which the distribution of both morphological and neural features related to the behaviors is included. Only by the examination of many such case studies will general patterns in the evolution of behavior emerge.

ACKNOWLEDGMENTS

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