BIOMECHANICS
IN EVOLUTION

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Biomechanics and evolution: integrating physical and historical biology in the study of complex systems

One of the key problems in the study of biomechanics and evolution is that posed by Darwin: how do complex structures and functions evolve? If the form and function of parts of organisms are tightly integrated, then how easy is it for complex structures to be modified in evolution? Two approaches, not mutually exclusive, have been applied to the problem of complexity. First, biomechanical or biophysical analysis has been applied to organisms to elucidate the relation between environmental demands and the design of morphological systems. Such analyses contribute both an understanding of the design constraints on organismal form and explicit mechanical or mathematical models of organismal function. Second, historical, phylogenetic analysis has allowed the definition of evolutionary sequences of structural and functional change in organisms. In this chapter, two possible research programmes that integrate historical and biophysical analysis are presented. The first addresses the question of the relations among evolutionary change at different levels of biological organization: how independent is evolutionary change in form, function and behaviour? The second research programme uses biomechanical models to provide a causal theory that forms the basis for interpreting historically correlated changes in form, function and behaviour. By integrating physical and historical approaches to complex organismal design, we will be able to resolve the problem of complexity raised by Darwin.

Introduction

A central fact confronting biologists and engineers as they attempt to understand organismal form and function is the apparent complexity of animal and plant design. Even the simplest structure is composed of many materials, may have more than one function, may be used by the organism in many ways, and has an evolutionary history which is not accessible to direct experimental analysis. More complex structures pose even greater problems as we attempt to provide scientific explanations for both the current diversity of biological form and function and for the historical patterns and processes that have produced this diversity. Complex morphological systems, because of their many parts, the intricacy of the interactions among the parts, and the difficulty of isolating individual components for study, have long been both a source of frustration for biologists and a magnet to which we are drawn in an attempt to apply the latest techniques and analytical tools. If we can understand the relation between form, function and the historical processes that have produced current diversity in a few complex morphological systems, then we will have made significant progress in our attempts to understand the causal basis of organismal design. This is an ultimate goal of many studies of biomechanics and evolution, the topic of this volume.

The 'problem of complexity' was well known to Darwin, who felt that complex morphological systems posed a special difficulty for his theory of evolution by natural selection. In a chapter outlining possible difficulties with his theory, Darwin (1859, chapter VI, pp. 186–187) discussed the eye, noting that it is difficult to imagine how such a complex structure could have been formed by a series of small structural and functional modifications. Indeed, it *is* difficult to imagine how the eye 'with all its inimitable contrivances for adjusting the focus to different distances, for admitting different amounts of light, and for the correction of spherical and chromatic aberration' (Darwin 1859, p. 186) could be modified in stages and how individual parts could be changed without disrupting the function of the entire structure.

A key concept underlying the problem of complexity, both as seen by Darwin and in modern formulations, is that organisms are highly integrated systems. How is it possible to change just one component of a structurally and functionally integrated unit? It is easy to imagine that altering one part of a complex structure could render the whole non-functional or at least of greatly reduced efficiency. The more tightly integrated are all the structures and functions of a complex system, the more difficult it should be to modify any single component.

The idea that organisms are highly integrated systems in which modification of one small feature has consequences for all the other structures and functions has been manifested many times in the history of biology (Russell 1916). Cuvier, for example, felt that all morphological features were so highly correlated and interrelated that by finding just one small part of a new fossil animal he could predict the form of the remaining parts. Russell (1916, p. 35) summarizes Cuvier's views by commenting that 'Cuvier's famous principle of correlation, the cornerstone of his work, is simply the practical application to the facts of structure of the principle of functional adaptedness. By the principle of correlation, from one part of an animal, given sufficient knowledge of the structure of its like, you can in a general way construct the whole.' Quoting from Cuvier (1826, p. 310), Russell continues, 'This must necessarily be so: for all the organs of an animal form a single system, the parts of which hang together, and act and react upon one another; and no modifications can appear in one part without bringing about corresponding modifications in all the rest.' More recently, similar views have been expressed by Taylor & Weibel (1981) and Weibel (1984), who advocate an extreme view of optimal design and intercorrelation among parts in the design of the mammalian respiratory system: 'in a functional system as complex as the one we are considering there is important interaction and cross-influence from one part to the other' (Weibel 1984, p. 60). These authors view all levels of organismal design, from cells to tissues and organs, as being coadapted so that changes at any one level necessarily entail alterations in structure and function at other levels.

This chapter addresses the problem of complexity in the context of studies of biomechanics and evolution. If organisms are in fact highly integrated systems in which any one part is difficult to alter without changing all the others, then it is indeed difficult to imagine how historical changes could take place in complex morphological systems. On the other hand, if there is considerable flexibility in complex systems such that characters and individual components of complex designs can be changed independently of other parts, then it is easier to envisage how changes in a complex structure could be achieved. In essence, this suggests that a central question in biomechanics and evolution today is: how many degrees of freedom does any complex morphological system possess? If there are few degrees of freedom, then complex designs should be relatively stable through time and changes in parts highly correlated with each other. If there are many degrees of freedom, then any one part of a complex design should be alterable without affecting other components.

Physical and historical biology

Over the last twenty years two main approaches have been taken toward understanding complex organismal designs. The first is the biomechanical or biophysical approach (physical biology), while the second is the historical or evolutionary approach (historical biology). The two avenues are by no means mutually exclusive, but they have not often been applied by the same investigator to any one morphological system.

Physical biology is well exemplified by several chapters in this volume and by the works of Wainwright *et al.* (1976), Alexander (1968, 1971), Currey (1970), and the classic volume of Thompson (1917). The main goals of this approach are to define extrinsic constraints on animal design by precisely formulating both the physical and mechanical properties of biological materials and of the environment experienced by organisms. By precisely specifying in mathematical terms the demands of the environment on biological systems, and by then examining the mechanical design of organisms quantitatively, it is possible to determine the extent to which organismal design accurately matches environmental demands. Particularly good examples of this type of analysis include studies of animal flight (Rayner 1981, 1985; see also Wootton & Ellington, Riess & Frey, Padian and Rayner, this volume).

Historical biology, on the other hand, has had as a major goal the definition of precise historical sequences of structural and functional change (Lauder 1981, 1982*a*). This goes beyond the inference of functional attributes of fossils based on living species and biomechanical models in an attempt to document and explain historical sequences of change in an explicitly phylogenetic framework. Thus, not only are historical biologists interested in how a particular animal (either living or fossil) worked, but also in the exact historical sequence by which a particular morphological design was constructed.

A simple hypothetical example to illustrate an historical approach to organismal design is shown in figure 1. A hypothetical complex morphological system (shown at the top) is composed of a number of bones (indicated by circles), ligaments (broken lines), and muscles (black lines). This is the configuration possessed by species A. The phylogenetic relationships of species A and several closely related species (B to G) are shown underneath. After a phylogeny for these species has been obtained, the morphological configuration of each species is determined (by dissection, for example). Mapped onto the phylogeny is the level at which several of the morphological links of the complex design above evolved. Thus, species A, B, C, D and E all share the presence of muscle 4, while species G and F lack it. Muscle 4 is then considered to have evolved between nodes 4 and 3 and its occurrence diagnoses species A to E as forming a natural (monophyletic) lineage. Muscle 4 and ligament 6 form one biomechanical pathway (i) between bones c and d, while muscles 10, 9 and ligament 7 form a second (ii) biomechanical pathway (figure 1*a*). In species A, and only in species A, bone d can be moved by either (or both) of biomechanical pathways i and ii.

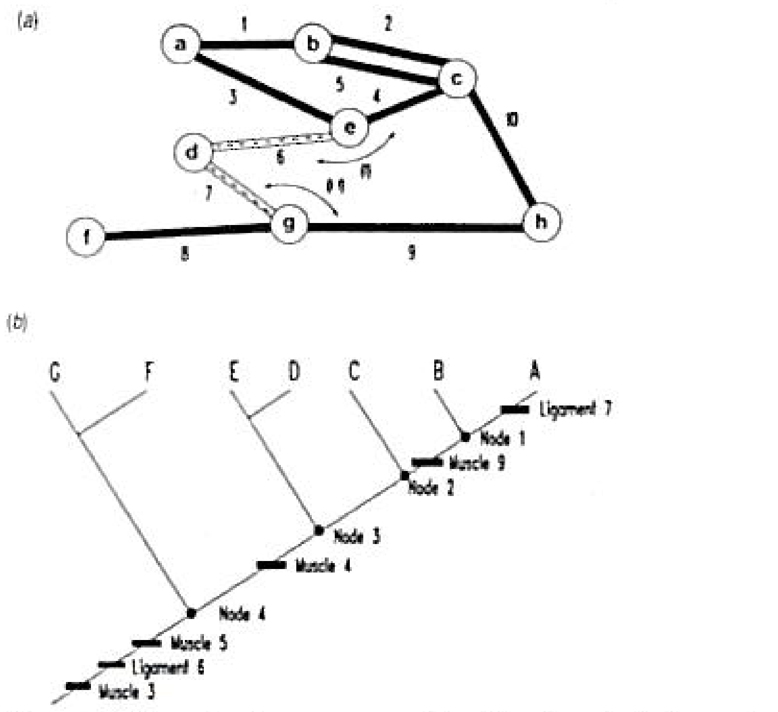

Figure 1. Schematic diagram representing (*a*) a hypothetical complex morphological system and (*b*) the historical sequence by which it was built up. Bones are represented by circles labelled with lower-case letters. Ligaments and muscles are numbered and are indicated by broken lines and black lines, respectively. Two pathways, numbered (i) and (ii), indicate two biomechanical linkage systems for moving bone d. (*b*) The phylogenetic relationships of seven species (A to G) with the historical origin of several components of the complex morphological system of (*a*) indicated. The diagram in (*a*) shows the morphology of species A in (*b*).

The phylogenetic analysis (figure 1*b*) indicates that the biomechanical control of bone d evolved by a two stage process. First, pathway i arose, becoming complete by node 3 with the addition of muscle 4. All species at or above node 3 have the ability of moving bone d by pathway i. Then, pathway ii evolved, the first step being the addition of muscle 9 to the design, and the second, final, step being the addition of ligament 7 after node 1.

This type of analysis is fundamentally important in studies of biomechanics and evolution for several reasons. First, and most basically, it demonstrates the exact historical sequence by which the morphological design in species A was constructed. Second, it places considerable constraints on the types of allowable explanation for why the morphological design possessed by any of these species evolved. For example, any hypothesis that species C is adapted to function in a particular environment because of its morphology must also account for the fact that species D and E share the same morphology. Thus, the environment that is historically correlated with the single pathway i in species C is actually that environment present at node 3 on the phylogeny. If species A experiences the same environmental forces as species B to E, then it has simply retained a primitive ecological pattern that is not correlated with the evolution of two morphological novelties (muscle 9 and ligament 7). By focusing our biomechanical models and analyses on only one species and its present day environment, we may mistake a current correlation between form and environment for a causal relationship. The historical, phylogenetic analysis thus allows us to reject many proposed correlations as spurious, but does not itself enable us to establish a causal connection. How this can be done is discussed in more detail below.

Some attempts have been made to integrate both analyses of historical patterns and biophysical attributes of organismal design (see, for example, Kingsolver & Koehl (1985), Gans (1960, 1968), Lauder (1983, 1986), Liem (1973), Lombard & Wake (1986) and Schaefer & Lauder (1986)). But, in general, there has been little effort to develop case studies explicitly (an area where this symposium will be particularly valuable) and conceptual methodologies for integrating historical and biophysical approaches to organismal design.

In this chapter, I will outline two areas in which integrating physical and historical approaches could make significant contributions to our understanding of the problem of complexity and to the biomechanics and evolution of organismal design.

The first area involves the problem of complexity: how tightly integrated are organisms? Are changes in one component of a complex system necessarily reflected in other parts? Are changes at one level of biological organization reflected at other levels? A major contribution toward resolving the problem of complexity will be to determine the extent of integration in organismal design.

The second area concerns the conceptual role that biomechanical models and analyses play in analysing historical patterns to biomechanical design. Can biomechanical models be used as a causal link between historical correlations in patterns of structural, functional and behavioural/ecological change? If so, such biomechanical analyses will play a crucial role in conjunction with historical analysis in helping us to avoid the pitfalls of a purely correlational approach to the evolution of design.

These two areas will now be considered in turn, with the general aim of illuminating the relation between biomechanical and evolutionary analysis.

Table 1. *Levels of analysis of complex morphological systems*

Level of analysis	Structures/functions to be studied
1 Behavioural	Movements and movement sequences
2 Peripheral morphology	Anatomy of the musculo-skeletal system
3 Motor pattern	Pattern (sequence and timing) of central nervous output to the peripheral musculature
4 Central nervous system structure	Anatomy of brain and spinal cord nuclei and their interconnections
5 Central nervous system circuits	Neural networks and the pattern of neuronal excitation

Evolution at different levels: behaviour, structure and function

One way to analyse the extent to which any complex morphological system forms an integrated whole is to break it down into multiple levels and ask if any one of these levels can be modified independently of the others. In the context of animal biomechanics and evolution there are several natural levels into which one can divide a complex system. Table 1 illustrates several of these levels.

Any complex morphological system is used by animals to perform behaviours, and the behavioural level (table 1: level 1) is perhaps the most general level at which one might study form and function. If one is interested in studying the form and function of bird wings, then this level of analysis might involve analysing the kinematic patterns of wing strokes during flight, mating behaviour, feeding and nesting. Behavioural acts such as these have a morphological basis, systems of muscles and bones that are directly responsible for the kinematic patterns seen, and this forms the next level (table 1: level 2) at which one could study a complex morphological system. Continuing with the example of bird wings, one would then dissect the bones, muscles and ligaments of the wing and determine their form, interrelations and mechanical properties. In order to execute a behavioural act, the muscles must be activated by the nervous system in a particular pattern and with particular levels of force. The pattern of central nervous activation of peripheral musculature, called the motor pattern, can thus be analysed (table 1: level 3) to provide information at the next 'lower' level of organization. In the study of bird wings, the investigator would measure the sequence and amplitude of muscle electrical activity with electromyographic recordings of wing musculature during the behaviours of interest.

The motor pattern is communicated to the peripheral musculature by the

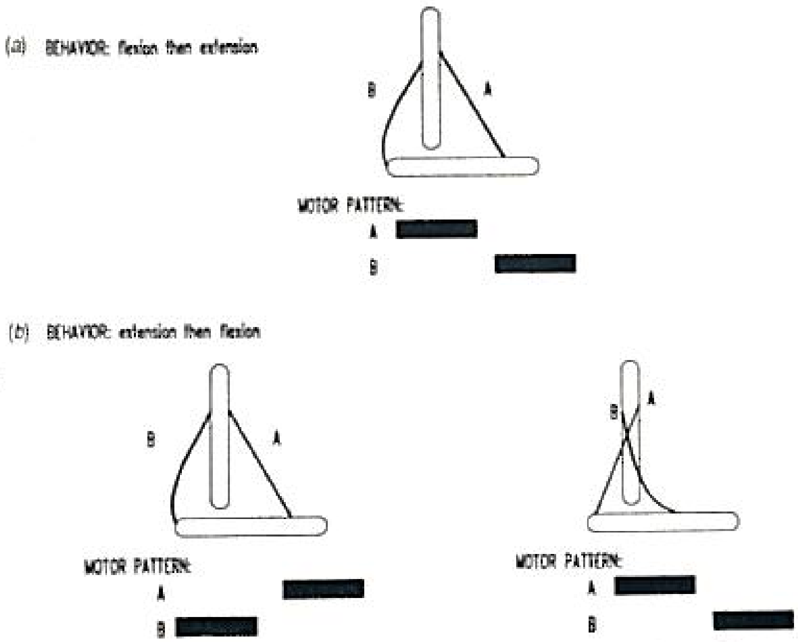

Figure 2. Diagram of two bones in several hypothetical species, and two muscles (black lines), A and B, moving those bones. (*a*) One species in which a behaviour, flexion followed by extension, is produced with the motor pattern shown; muscle A contracts for a time (indicated by the black bar) and then muscle B contracts. (*b*) Two alternative ways for a novel behaviour, extension followed by flexion, to be produced. This behaviour could be produced by altering the motor pattern such that muscle B contracts before muscle A (left), or by altering the peripheral morphology and retaining the same motor pattern (right). Muscle B now causes flexion because of alterations in its insertion.

central nervous system, and one could carry the analysis of any complex morphological system into the nervous system (table 1: level 4) to study the interconnections of nerve nuclei that are responsible for the motor pattern studied previously. Thus, one might make horseradish peroxidase injections into the peripheral muscles of the bird wing and study the central projections of the motor neurons to these muscles. Finally, one might want to use electrophysiological techniques to carry the analysis down to the cellular level in the nervous system and determine the precise neuronal circuit that produces the motor pattern (table 1: level 5). Of course, neuronal circuits have their origin in the biophysical properties of nerve cells and cell membranes (not shown in table 1), and this is yet another potential level of analysis.

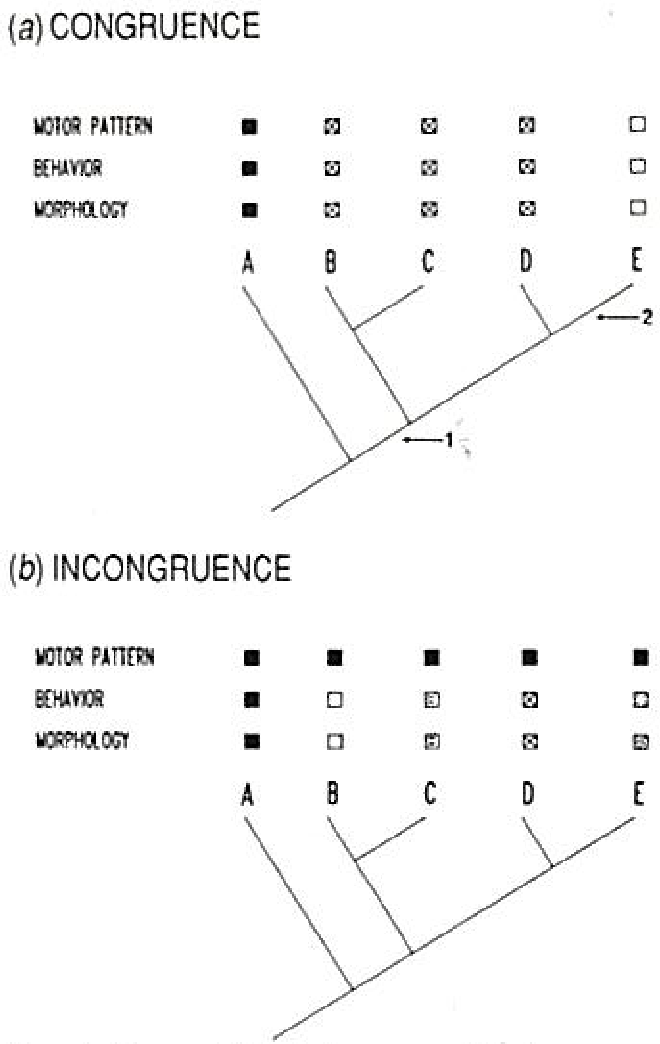

Figure 3. Diagram of historical congruence (*a*) and non-congruence (*b*) in the evolution of levels of morphological design. For the sake of simplicity, only three of the levels outlined in table 1 are shown. The arrows in (*a*) indicate the phylogenetic level at which congruent change occurred. In (*b*) the motor pattern has remained phylogenetically conservative, while behaviour and morphology have changed. This is a non-congruent pattern of historical transformation in levels of organization.

If complex morphological systems are truly integrated, and if the correlation among parts in such systems is high, then one would expect that a change at any one of these levels would necessitate a change in other levels. On the other hand, if a particular complex system is loosely integrated, then one would predict that changes could occur in any one of these levels without

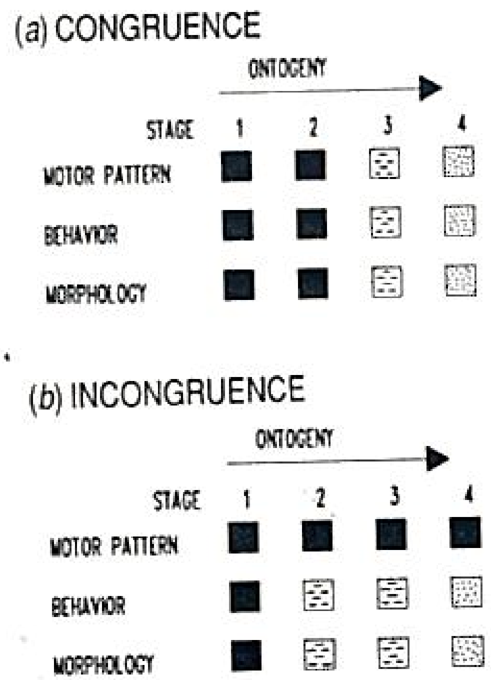

Figure 4. Diagram of (*a*) ontogenetic congruence and (*b*) non-congruence in the transformation of levels of morphological design. In (*a*) modification of three levels of design occurs congruently across ontogenetic stages. Changes in all three levels occur between ontogenetic stages 2 and 3, and between stages 3 and 4. In (*b*) one of many possible non-congruent patterns is shown, in this case with the motor pattern remaining conservative throughout ontogeny.

substantially affecting the others. Levels of design may thus be decoupled from one another.

We may now state an important problem in biomechanics and evolution: *to what extent are changes at different levels of biological design independent of one another during ontogeny and phylogeny*?

A simple example will serve to illustrate how changes could occur at one level independently of another level (figure 2). One species (figure 2*a*) has a morphological system composed of two bones connected on each side by two muscles, and exhibits a behaviour of flexion followed by extension. This results from the motor pattern shown (figure 2*a*): muscle A contracts followed by muscle B. Another closely related species might exhibit a different behaviour: extension followed by flexion. This could result from changes either at the motor pattern level or at the peripheral morphology level (table 1; figure 2*b*). A simple reversal in the motor pattern such that muscle B is activated prior to muscle A would produce the reversal of the behaviour seen in species A (figure 2*b*). A change at the motor pattern level would thus affect behaviour without affecting other levels. Alternatively, the motor pattern could remain the same, with the new behaviour in species B being entirely the result of alterations in the design of the peripheral musculo-skeletal system. If muscle A moves to attach to the opposite side of the bone, and muscle B does the same, then the motor pattern of species A will have the effect opposite to that which it used to have (figure 2*b*).

Depending on which of these results was obtained in a comparative analysis of these two species, one would say that either the motor pattern or the peripheral musculo-skeletal system was conserved in the evolution of these species.

The analysis of these different levels of design (table 1) involves physiological and biomechanical techniques to determine the structure and function appropriate for each level. However, to discuss the modification of these levels, we need to introduce an historical or ontogenetic analysis. For an historical analysis, the question of which levels are modified independently of others (if any) reduces to the following question: *are changes at different levels of design phylogenetically congruent*? This question can be answered by mapping changes in these different levels onto a phylogeny of a group of related species. Figure 3 shows two simple examples. If changes at the motor pattern and musculo-skeletal levels are decoupled historically, then one would expect to see a phylogenetic pattern where changes in these two levels at successive hierarchical nodes are not concordant (figure 3*b*). Alternatively, historical concordance, indicating that complex morphological systems are highly integrated, would result in a congruent pattern (figure 3*a*) where changes at any given node involve many levels of design.

A similar analysis could be conducted ontogenetically, and examples are shown in figure 4. Again, if all levels of organismal design are highly integrated, then when behaviour changes during ontogeny we expect to see concomitant changes at lower levels (figure 4*a*). On the other hand, non-congruent changes at the different levels would produce the pattern shown in figure 4*b*.

To date, no analyses have been completed even for one case study that would enable us to say unequivocally whether changes at *all* these different levels are congruent or not during ontogeny and phylogeny. However, two sets of ongoing research projects, involving both ontogenetic and phylogenetic analyses, allow us to address these issues at least for some of the possible levels of analysis. These studies involve the functional morphology and biomechanics of prey capture in lower vertebrates.

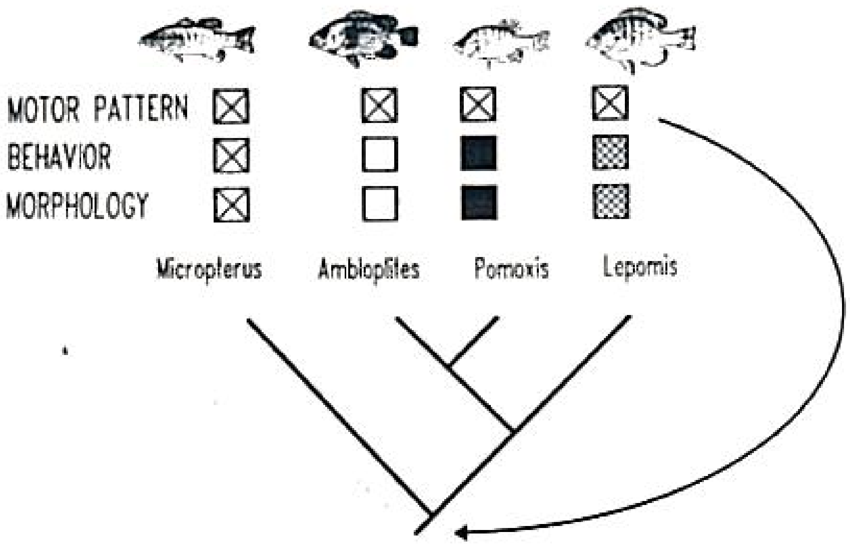

Figure 5. Diagram of the phylogenetic relationships of four genera of sunfishes (Centrarchidae) after Humphries & Lauder (unpublished results). Despite differences in mouth shape and size and differences between genera in feeding performance on different prey, the motor pattern used by these genera is extremely similar (Wainwright & Lauder 1986). Only one of eleven variables measured from the feeding motor pattern in four cranial muscles differed among the genera. Thus, the motor pattern is a primitive feature of this clade, as indicated by the arrow.

First, feeding behaviour in fishes has been used as a case study in the phylogenetic transformation of a complex morphological system, the feeding mechanism (Lauder 1980, 1982*b*, 1983, 1985; Wainwright & Lauder 1986). Second, we have used the ontogeny of feeding behaviour in tiger salamanders as a system to investigate ontogenetic congruence among behavioural, musculo-skeletal and motor pattern levels (Lauder & Shaffer 1986; G. V. Lauder & H. B. Shaffer, unpublished results; Shaffer & Lauder 1985*a*,*b*).

The results from a biomechanical and phylogenetic analysis of prey capture in sunfishes, an endemic North American family containing about 32 species, are shown schematically in figure 5. The phylogeny of the four genera shown derives from work by Humphries & Lauder (unpublished results). Each of the four genera differs considerably from the others in the gross morphology of the mouth (figure 5) and in feeding performance on different prey. For example, the bass (*Micropterus*) feeds on minnows to a greater extent than the other species and has a large gape and an enlarged mouth cavity, especially relative to genera such as *Lepomis*. Thus, the genera shown differ considerably in feeding behaviour and morphology. Wainwright & Lauder (1986) conducted an analysis of the muscle activity pattern (motor pattern) used by these species to determine if they differed. Small electrodes were implanted in four head muscles while the fishes were anaesthetized, and the fishes allowed to feed when they had recovered. The relative timing and duration of electrical activity in four head muscles involved in opening and closing the mouth was measured in all four genera. Statistical analysis showed that the motor pattern used by the four genera during prey capture was extremely similar, differing in only one of eleven variables (Wainwright & Lauder 1986). This case study argues strongly that the differences seen among the species in feeding performance and behaviour are a consequence of the morphological differences among the species, not of any differences in the neural output to the musculature. Behavioural variation in this clade is thus a consequence of morphological variation, not of changes in the output of the nervous system.

The results of our work on the ontogeny of feeding behaviour in salamanders is summarized in table 2. In these studies, the feeding behaviour of tiger salamanders (*Ambystoma tigrinum*) was studied during ontogeny. Larval tiger salamanders feed in the water by using suction feeding (Lauder 1985; Lauder & Shaffer 1985): prey are captured by rapidly expanding the volume of the mouth cavity (creating a negative pressure) and drawing water and the prey into the mouth. After metamorphosis, tiger salamanders will feed either on land or in the water.

Among numerous morphological changes in the feeding mechanism at metamorphosis, the most significant is the change from a unidirectional to a bidirectional feeding system (Lauder & Shaffer 1986). Larval tiger salamanders feed by drawing water into the mouth anteriorly and expelling it over the gill slits posteriorly. Water flow through the mouth is thus unidirectional, from anterior to posterior. During metamorphosis the posterior gill openings close off, eliminating the exit for water. Thus, when metamorphosed animals feed in the water, they must expel the water captured with the prey anteriorly through the mouth, and flow is bidirectional.

The transformation to a bidirectional feeding design results in greatly reduced feeding performance in metamorphosed tiger salamanders feeding in the water (table 2): larvae are much more efficient at capturing elusive prey (Lauder & Shaffer 1986). The results of G. V. Lauder & H. B. Shaffer (unpublished) show that there has been no change in the pattern of electrical activity in the jaw muscles with metamorphosis. Thus, the motor pattern does not change with metamorphosis, despite major changes in the morphology of the feeding mechanism (table 2).

Table 2. *Changes in the feeding system of* Ambystoma tigrinum, *comparing larvae feeding in the water with metamorphosed animals feeding in the water*

Level of analysis	Change from larva (aquatic) to metamorphosed (aquatic)	Comments
1 Behavioural/performance	Yes	Larvae have higher performance
2 Peripheral morphology	Yes	Major changes in the hydrodynamic design of the feeding mechanism
3 Motor pattern	No	Electro-myography of six jaw muscles shows no changes between these two stages

Although neither of these case studies has yet been developed to the point where we can unequivocally say that the only change that produces an alteration in behaviour or performance is at the peripheral morphological level, both case studies strongly indicate that the motor pattern used to produce behaviour may be very conservative in ontogeny and phylogeny. It is thus not necessary to alter this level of biological design to effect a novel behavioural pattern. To this extent, then, we may say that complex morphological systems such as the feeding apparatus in lower vertebrates may change in behaviour (performance) without any necessary concomitant alteration in motor pattern.

Biomechanical analyses as causal links

It is common for biologists interested in particular morphological features or behaviours to propose explanations for why these structures or behaviours have arisen, and to propose that the acquisition of a morphological feature conferred a particular selective advantage to the individuals or species that possessed this feature. Such hypotheses can be very difficult to test. However, it is possible to define two criteria (involving both historical and biomechanical analyses) which can serve as a set of boundary conditions on hypotheses that certain structures confer advantages or allow new behaviours.

If several species share the presence of a certain feature, such as a shortened humerus, one might wish to propose that this shortening confers an increase in digging efficiency in those species with the shorter bone. If one further wished to propose that the shortening of the bone is an adaptation for digging that arose and has been maintained in evolution because of the functional advantage obtained by shortening the humerus, then at least two criteria need to be met.

First, the feature proposed to confer the functional advantage must have arisen phylogenetically in a congruent fashion with the improved behavioural efficiency (figure 6*a*). This contrasts with the situation in which the morphological feature has an incongruent origin with the behavioural advantage (figure 6*b*). Historical discordance in origin of the morphology and the behaviour refutes any hypothesized advantage attributable to the morphological feature. As discussed by Greene (1986), it is minimally necessary for hypotheses of adaptation that historical concordance be true for the characters under consideration.

However, the criterion of historical concordance alone is insufficient to demonstrate a causal connection between morphological features and behavioural advantage. As shown in figure 6*c*, there are *many* derived morphological features at each phylogenetic level. On any corroborated phylogenetic hypothesis, there are numerous shared derived attributes that characterize lineages. Which of these many features is related to the behavioural shift shown by species A, B and C (figure 6*c*)? Without an external covering law or model (Hull 1974) there is no way to distinguish which of the many *correlated* characters that arose at a particular phylogenetic level is in fact *causally* related to the change in behaviour.

Thus, the second criterion that needs to be met is that a biomechanical model be available that predicts precisely which morphological feature should cause the alteration in behaviour and why they should do so. This biomechanical model plays the role of a covering law: it provides an external standard by which to separate out correlated from causal relationships (figure 6*d*).

Returning to our example of digging behaviour and the shortening of the humerus, we may find that indeed both an increase in digging efficiency and shortening of the humerus have a correlated historical origin. (This would be determined by examining bone length and digging speed in each of the six species shown in figure 6*a*; species A, B and C, and only these species, should share both decreased humerus length and increased digging speed.) Even though the criterion of historical congruence has been met, we still have no evidence that in fact the decreased length of the humerus has *caused* the increase in digging efficiency unless we can produce a biomechanical model that predicts *a priori* that shortening the humerus should produce an increase

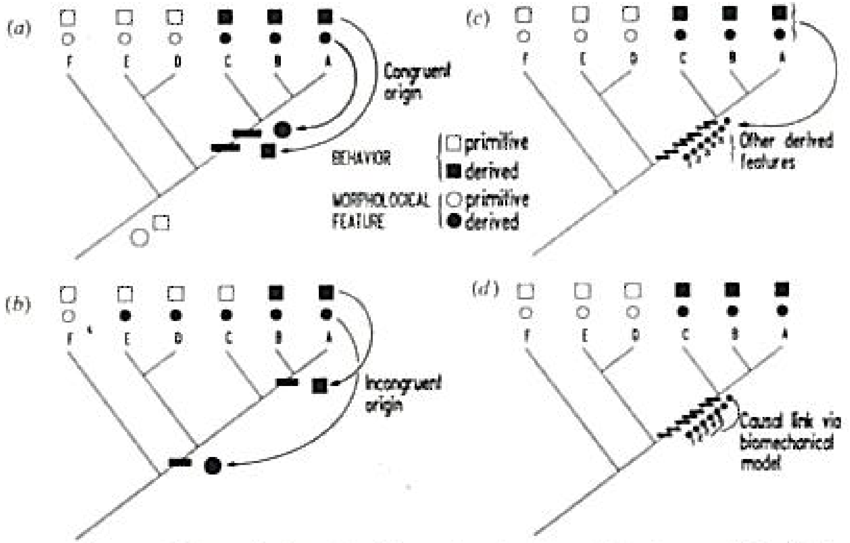

Figure 6. Four phylogenies illustrating the idea that the analysis of the historical relation between morphological and behavioural features is incomplete without a biomechanical model describing the causal linkage between specific morphological features and the behaviour. In all parts of the figure behaviours are indicated by boxes and morphological features by circles; derived states are represented by filled symbols. The transition from open to filled symbols indicates the origin of a novel feature. Open symbols characterize the ancestral condition in all panels. (*a*) Phylogenetic relationships of six species (A to F). Three species, A, B and C, share both derived behavioural and morphological conditions relative to ancestral traits. Both these traits are inferred to have evolved together prior to the origin of species C, as indicated by the arrows and black bars on the phylogeny. (*b*) Theoretical case where the distribution of a particular morphological feature is wider than that of a behaviour possessed by species A and B. The historical origin of the morphological and behavioural features (arrows) is incongruent, in contrast to the situation in (*a*). (*c*) At any level on a phylogeny, there will be many characters (out of the infinite number that organisms possess) that have evolved concordantly (indicated by filled circles 1 to 5), and thus many characters that are correlated with the historical origin of a particular behavioural feature. (*d*) Only some of those features sharing an historical origin with a behavioural feature (in this case filled circles 3, 4 and 5) will be predicted by any given biomechanical model to be causally related to the behavioural feature. Only then can we ascribe causal relations to the congruent origin of morphological and behavioural features.

in digging efficiency. This second criterion of biomechanical causation must be met in order for us to have any confidence in arguments for historical adaptation. In the digging example, such a biomechanical model might take the form of a diagram resolving the impact forces on the forelimb when the hand contacts the ground. This model could be used to predict the mathematical relation between length of the humerus and the force applied to the ground. If the model were sufficiently general, then it could also be used to evaluate the effect of changing other morphological features (such as the length of each of the other limb bones) on the force produced on the ground.

Conclusions and prospectus

In this chapter I have focused on two areas in which biomechanical and historical analyses can be mutually illuminating. These are areas that have not received much attention to date, but which have considerable potential for guiding future research.

Both biomechanical and historical analyses are needed in our attempts to clarify the problem of complexity raised by Darwin, and to discover how ontogenetic and phylogenetic change occurs in complex morphological systems. If evolutionary change at different levels of organization is independent, then the 'problem of complexity' raised by intricate organs such as the vertebrate eye (Darwin, 1859) is greatly reduced.

Similarly, both biomechanical and historical analysis are needed to constrain and test hypotheses of adaptation. By integrating biophysical and historical approaches, we will be better able to make progress in understanding the actual causal factors underlying the diversity of organismal form and function.

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References

Alexander, R.McN. 1968 *Animal Mechanics*. Seattle: University of Washington Press.

Alexander, R.McN. 1971 *Size and Shape*. London: Edward Arnold.

Currey, J.D. 1970 *Animal Skeletons*. London: Edward Arnold.

Cuvier, G. 1826 *Histoire des Progrès des Sciences naturelles depuis* 1789. Paris.

Darwin, C. 1859 *On the Origin of Species*. London: John Murray.

Gans, C. 1960 Studies on amphisbaenids (Amphibia, Reptilia). I. A taxonomic revision of the Trogonophinae and a functional interpretation of the amphisbaenid adaptive pattern. *Bulletin of the American Museum of Natural History* **119**, 129–204.

Gans, C. 1968 Relative success of divergent pathways in amphisbaenian specialization. *American Naturalist* **102**, 345–362.

Greene, H. 1986 Diet and arboreality in the emerald monitor, *Varanus prasinus*, with comments on the study of adaptation. *Fieldiana Zoology* (N.S.) **31**, 1–12.

Hull, D. 1974 *Philosophy of Biological Science*. New Jersey: Prentice Hall.

Kingsolver, J.G. & Koehl, M.A.R. 1985 Aerodynamics, thermoregulation, and the evolution of insect wings: differential scaling and evolutionary change. *Evolution* **39**, 488–504.

Lauder, G.V. 1980 Evolution of the feeding mechanism in primitive actinopterygian fishes: a functional anatomical analysis of *Polypterus*, *Lepisosteus*, and *Amia*. *Journal of Morphology* **163**, 283–317.

Lauder, G.V. 1981 Form and function: structural analysis in evolutionary morphology. *Paleobiology* **7**, 430–442.

Lauder, G.V. 1982*a* Historical biology and the problem of design. *Journal of Theoretical Biology* **97**, 57–67.

Lauder, G.V. 1982*b* Patterns of evolution in the feeding mechanism of actinopterygian fishes. *American Zoologist* **22**, 275–285.

Lauder, G.V. 1983 Functional design and evolution of the pharyngeal jaw apparatus in euteleostean fishes. *Zoological Journal of the Linnean Society of London* **77**, 1–38.

Lauder, G.V. 1985 Functional morphology of the feeding mechanism in lower vertebrates. In *Functional Morphology in Vertebrates*, ed. H.-R. Duncker & G. Fleischer, pp. 179–188. Stuttgart and New York: Gustav Fischer Verlag.

Lauder, G.V. 1986 Homology, analogy, and the evolution of behavior. In *The Evolution of Behavior*, ed. M. Nitecki & J. Kitchell, pp. 9–40. Oxford University Press.

Lauder, G.V. & Shaffer, H.B. 1985 Functional morphology of the feeding mechanism in aquatic ambystomatid salamanders. *Journal of Morphology* **185**, 297–326.

Lauder, G.V. & Shaffer, H.B. 1986 Functional design of the feeding mechanism in lower vertebrates: unidirectional and bidirectional flow systems in the tiger salamander. *Zoological Journal of the Linnean Society of London* **88**, 277–290.

Liem, K.F. 1973 Evolutionary strategies and morphological innovations: cichlid pharyngeal jaws. *Systematic Zoology* **22**, 425–441.

Lombard, R.E. & Wake, D.B. 1986 Tongue evolution in the lungless salamanders, Family Plethodontidae. IV. Phylogeny of plethodontid salamanders and the evolution of feeding dynamics. *Systematic Zoology* **35**, 532–551.

Rayner, J.M.V. 1981 Flight adaptations in vertebrates. *Symposia of the Zoological Society of London* **48**, 137–172.

Rayner, J.M.V. 1985 Mechanical and ecological constraints on flight evolution. In *The Beginnings of Birds*, ed. M.K. Hecht, J.H. Ostrom, G. Viohl & P. Wellnhofer, pp. 279–292. Eichstätt: JuraMuseum.

Russell, E.S. 1916 *Form and Function, a Contribution to the History of Animal Morphology*. London: John Murray. [Reprinted, University of Chicago Press, 1982.]

Schaefer, S.A. & Lauder, G.V. 1986 Historical transformation of functional design: evolutionary morphology of feeding mechanisms in loricarioid catfishes. *Systematic Zoology* **35**, 489–508.

Shaffer, H.B. & Lauder, G.V. 1985*a* Patterns of variation in aquatic ambystomatid salamanders: kinematics of the feeding mechanism. *Evolution* **39**, 83–92.

Shaffer, H.B. & Lauder, G.V. 1985*b* Aquatic prey capture in ambystomatid salamanders: patterns of variation in muscle activity. *Journal of Morphology* **183**, 273–284.

Taylor, C.R. & Weibel, E. 1981 Design of the mammalian respiratory system. I. Problem and strategy. *Respiration Physiology* **44**, 1–10.

Thompson, D'A.W. 1917 *On Growth and Form*. Cambridge University Press.

Wainwright, P. & Lauder, G.V. 1986 Feeding biology of sunfishes: patterns of variation in prey capture. *Zoological Journal of the Linnean Society of London* **88**, 217–228.

Wainwright, S.A., Biggs, W.D., Currey, J.D. & Gosline, J.M. 1976 *Mechanical Design in Organisms*. New York: John Wiley.

Weibel, E. 1984 *The Pathway for Oxygen*. Cambridge, Massachusetts: Harvard University Press.