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Complex Organismal Functions: Integration and Evolution in Vertebrates

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Group Report

How Are Feeding Systems Integrated and How Have Evolutionary Innovations Been Introduced?

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INTRODUCTION

The nature and extent of integration in complex structural systems is a long-standing problem in biology. Predarwinian morphologists (e.g., Cuvier) recognized the problems posed by structural systems composed of many parts, with each of the elements linked to each other and involved in complex movements. The recognition and description of complex integrated systems was an important stimulus for the development of predarwinian theoretical concepts in morphology such as the "law of correlation of parts" and the "hierarchy of functions."

As is well known, Darwin (1859) highlighted the problem of complexity in the *Origin of Species* when he discussed "organs of extreme perfection and complication" at length, choosing the vertebrate eye as a key example. How can a structural system displaying a high degree of order and complexity be created or changed? Might not a network of interacting elements be difficult to modify when the function of the system as a whole depends so intimately on the coordinated functioning of the parts?

The role of our group was to focus on the problem of integration and transformation in complex systems using the vertebrate feeding mechanism as an example. The vertebrate feeding system constitutes a complex system par excellence. In some vertebrates, for example, the capture of prey may involve the coordinated movement of as many as 50 separate bones within a time frame of 20 milliseconds. Extensive modification in trophic design has been a prominent feature of vertebrate diversification, and the acquisition of energy from the environment is clearly a process of considerable importance to organismal fitness.

Our group defined four specific goals. First, we felt that it was important to clarify terms and general concepts that form the basis of discussions about the structure and function of complex systems. Second, we endeavored to outline the major methods used to analyze vertebrate feeding. Third, we attempted to identify common themes underlying changes in integration of feeding systems. Fourth, we strove to arrive at several general conclusions about the integration and evolution of feeding systems, and to present recommendations for future research.

A recurrent theme in our discussions was the fact that only a few case studies exist on vertebrate feeding systems. While several of these provide considerable insight into the nature of integration in complex systems, feeding in the broad diversity of vertebrates is woefully underrepresented in the current literature. In order to test the generality of the ideas discussed below it is essential that future studies systematically characterize a diversity of vertebrate clades and that the mechanics of feeding be analyzed quantitatively.

TERMINOLOGY

Causation

The group recognized that analysis of the *causes* of structural change frequently is a complex undertaking. Whereas the statement that A causes B implies a deterministic process or mechanism (that does not necessarily answer the question "why?"), we wish to emphasize the importance of distinguishing multiple meanings of the word "cause" and to focus attention on the original Aristotelian distinctions. If, as explained by Aristotle, a carpenter wants to build a closet, the wood he uses is the material cause (*causa materialis*), the power of his hands is the efficient cause (*causa efficiens*), the plan according to which he builds his closet is the formal cause (*causa formalis*), and the end which the closet is designed to serve is the final cause (*causa finalis*). Several meanings of "cause" may apply when we discuss a particular structure in the feeding mechanism, especially if we focus on the developmental, genetic, and phylogenetic aspects of structural features. In addition, there are multiple levels of causation in any historical explanation. Any one hypothesis might address only a single level.

Function and Biological Role

The group felt that it was important to distinguish between the concepts of "function" and "biological role." These two concepts are frequently confused, especially in behavioral literature where "function" is used as a synonym of selective or adaptive value (see Lauder 1986).

The function of a structure is what the animal is physically capable of doing with that structure: the actual actions of phenotypic elements. The biological role of a structure reflects the use of part of the phenotype during life history and the hypothesized adaptive "purpose" of the structure in a given environment (Bock and von Wahlert 1965).

Complexity

The group agreed that no single measure of complexity was adequate for biological systems and that any biological system might, by definition, be considered complex. Whereas complexity may refer (at least) to (a) the number of elements in a system, (b) the number and kind of developmental processes that form structures, (c) the number of connections among elements, and (d) the type of connections, in general, the specific problem at hand will dictate the appropriate measure of complexity. Overall, we felt that it was important to use the concept of complexity in a comparative sense and to be aware that structurally simplified systems may, in fact, be highly complex functionally.

Integration

As with the concept of complexity, we felt that the idea of "integration" has no one definition that will apply in all cases. The extent of integration in any structural system, such as the feeding mechanism, might depend on the extent of interactions among the constituent elements, the number of reciprocal influences, and the extent of genetic correlation among phenotypic traits. Whereas the whole organism may be one appropriate level of integration, for specific subsystems the extent of integration may be estimated using quantitative genetic methods, morphometric approaches, and functional morphological techniques (Atchley et al. 1982; Zelditch 1987; Lauder and Liem, this volume; Olson and Miller 1958; Zweers 1979).

Because of the important role that genetic data have in discussions of the idea of integration, it is necessary to emphasize that different investigators may use the term "genetic" in quite dissimilar ways. In the field of population genetics, "genetic" may refer to all heritable variation in traits, and thus include both genetic and epigenetic information. To others, genetic data are those provided directly by genes.

Decoupling and Coupling

The idea of the decoupling of components in the feeding mechanism refers to the unlinking of developmental pathways, tightly linked functions, aspects of stereotyped behavior patterns, mechanical associations of bones, ligaments,

and muscles, or the reduction of a high genetic correlation. The concept of decoupling of elements of biological design has many aspects to it. If one structure is used to perform two functions in a clade, for example, then the shift of one of these functions to another structure is said to have decoupled the two functions from their initial association. Each of the two structure-function systems is now available for independent specialization in descendant taxa. The concept of a coupled system carries with it the idea of a constraint. If two systems are linked together (via a high genetic correlation, developmental interactions, or a joining muscle or ligament), then it will be difficult to change one part independently of the others. Because the decoupling of systems primitively linked in a clade provides a mechanism for releasing constraints, one would predict that clades possessing decoupled components (in comparison to sister clades with coupled systems) would exhibit increased structural/functional diversity in those systems. This view of decoupling by no means rules out a subsequent historical coupling of components. Indeed, in many lineages, primitively decoupled components may subsequently become highly integrated.

Several examples of decoupling were provided from feeding systems in which two (or more) mechanical linkages or functional systems are coupled in one clade, as compared to other clades where the connections are absent (see Lauder 1981; Liem 1987; Zweers 1985). In most avian orders, for example, nonmuscular scraper-like flaps with keratinous spines are present dorso-caudal to the larynx. These scrapers passively transport food into the esophagus during swallowing and food transport is thus coupled to swallowing. In pigeons and songbirds, however, these scrapers are decoupled from the larynx and possess separate controlling muscles. This anatomical decoupling of scrapers and the larynx is proposed to be causally related to increased flexibility of movement and a change in integration in avian feeding systems (Zweers 1985).

The general concept of a decoupling of structures and functions that may allow independent specialization of one or more of the components is not a new one. In the *Origin of Species* (1859, pp. 190–191), Darwin clearly recognized the importance of multiple structures and functions in permitting structural diversification. He emphasized that if multiple organs perform the same or similar functions, then one of the organ systems is able to be modified to acquire a new function.

MAJOR CONCEPTS UNDERLYING THE STUDY OF INTEGRATION IN FEEDING SYSTEMS

Our group considered five major ideas that underlie the study of integration in feeding systems. We felt that it was necessary to clarify several specific

concepts before we could discuss methodology and general hypotheses in a meaningful way.

Structuralism and Functionalism

The structuralist-functionalist dichotomy is one of the oldest in biology and is important in considering causal explanations of structure. While aspects of each view may be relevant to understanding organismal design, it is useful to outline the traditional tenets of each perspective.

The purely structuralist view of organismal design, as originally proposed, is tied to an ontogenetic time scale and is explicitly nonevolutionary (e.g., Piaget 1970). Structuralism is concerned with the unfolding of preexisting form during development, focuses on the generation of form, and addresses the efficient and material causes of structure. Such a structuralist might ask, "What is the driving and directing force of development?" or "What is the embryonic source from which adult structures develop?" In that sense most of the older research on comparative embryology is structuralist. Structuralism is often considered to be an "internalist" view of organisms as the focus lies on the design of structures, their interactions during ontogeny, and the interrelations among components of a design without regard for past or present environmental (extrinsic) influences on form.

The purely functionalist view, on the other hand, is tied to a phylogenetic time scale and addresses the formal and final causes of form. Structures are viewed as shaped primarily by external environmental factors. Such a functionalist might ask, "What has been the historical sequence by which this structure has been modified?," "What does this structure do?," or "How has this structure been molded by selective forces?" Structure is viewed as adaptive and not subject to significant intrinsic design constraints.

In our discussions, Wagner presented a useful analysis of the role of internal and external (environmental) influences on form as seen within the context of current evolutionary theory (Table 1). The combination of cells 2B in Table 1 represents a strict internalist view of form in which causes of change in structure are intrinsic to the organism and there is no apparent environmental influence on the system. The evolutionary increase in salamander genome size might represent one example (cf. Roth and Wake 1985). The strict functionalist/externalist perspective is illustrated by the combination of cells 1A in Table 1: organisms should have ample heritable variation in phenotypic traits but no strong genetic correlations among the traits. Under this view, there are no specific internal constraints on the direction of change in functional design. The current literature on the quantitative genetics of structural systems indicates that neither of the two extreme views presented above is represented by many real examples.

TABLE 1 Factors in the evolution of feeding systems. Letters and numbers in the table label each of the four cells to indicate combinations of factors and sources of change discussed in the text (after G. Wagner).

	External factors (i.e., environmental)	Internal factors
Cause of change	1	2
Direction of change	A	B

Examples involving combinations of these two extreme views are common, and cells 1B and 2A of Table 1 illustrate the two possible alternatives. The combination of 1 and B implies that the transformation of structure is caused by selection, while the direction of the transformation is constrained by the pattern of correlation or integration among elements. This may be the pattern most clearly supported by current data. With combination 2A, the environment may curtail or limit directions of change that arise due to internal factors within the organism.

Our discussions recognized the utility of clearly defining alternative research programs to the study of biological design, but also emphasized that the view of the organism represented by cells 1B or 2A would be necessary to understand the entire hierarchy of causation of form.

Phylogenetic and Population Analyses

The last twenty years have seen the rise of quantitative methods of phylogenetic reconstruction and quantitative analyses of the genetic basis of variation in characters; however, surprisingly few studies have bridged these two approaches. Most of the group felt that such a link was not only overdue, but also mandatory if ecological and genetic data are to be related in a nontrivial way to characterize evolution. However, not everyone agreed with this view, and the alternative view expressed was that making a link between ecological and genealogical hierarchies was logically flawed, as the unit of ecological analysis is the population, while the unit of phylogenetic analysis is the monophyletic clade.

For those who advocated increasing interactions among workers on populational and phylogenetic problems, three main advantages of a synthetic approach were identified. First, genealogical patterns provide the historical context for comparative biology and allow us to determine if characters (whether genetic, ecological, or structural) are shared due to common ancestry or due to convergent evolution. Second, phylogenetic hypotheses help solve problems of nonindependent observations (species) in comparative studies (Felsenstein 1985; Schluter, this volume) and provide a measure of

intercorrelation of points on an interspecific regression. Third, quantitative genetic analyses of the association of characters can be used to understand patterns of covariation of traits both on a cladogram and in an ecological setting.

Functional Compromises

There was general agreement among the group that feeding systems cannot be considered in isolation from the other functions performed by the head (such as respiration). The concept of a functional compromise is critical to understanding the transformation of feeding systems in vertebrates (Gans 1974).

Specific examples of functional compromises were discussed in the feeding systems of salamanders and fishes. In lung-breathing salamanders, the hyobranchial apparatus serves both as a force pump for the lungs and as the mechanism causing tongue movement during feeding (Roth and Wake 1985 and this volume; Wake 1982). The functions of breathing and feeding thus impose conflicting design requirements on the hyobranchial apparatus, constraining morphological diversification. In clades characterized by the loss of lungs, specialization of the hyobranchial apparatus for feeding function occurs, e.g., by developing a highly projectile tongue as in the case of the plethodontid tribe Bolitoglossini.

GENERAL APPROACHES

In our discussions, four analytical methods emerged as being of such importance to the analysis of integration in feeding systems that they are briefly described here.

Analysis of Ontogeny

The study of ontogeny is of obvious importance for our understanding of integration in feeding systems, but we wish to emphasize several key points.

First, the study of ontogenetic changes in feeding provides insights into embryonic and larval performance. Embryos often tend to be viewed as prospective adults and we often neglect to consider that early life history stages must also function as organisms. For example, the pattern of aortic arch development in tetrapods is often presented as a historically and developmentally constrained sequence of changes following a tortuous path toward adult form. But aortic arch components that are lost late in ontogeny may play an important role in nourishing developing tissue (such as jaw mesenchyme) and in embryonic circulatory mechanics. In addition, many

features of late ontogeny may be mechanically determined, an example being the sagittal crest in cats.

Second, comparative ontogeny provides a direct observational window into the modification of complex structures. The phylogeny of mammalian ear ossicles is a well-known example of a dramatic transformation that would be difficult to appreciate were it not possible to observe the ontogenetic process directly. The study of ontogenetic transformation clearly illustrates that extensive alterations in form and function can occur without disrupting the coherence of the organism.

Third, the experimental manipulation of ontogenies avoids the problems of differing historical constraints that arise in comparative analyses of species. While such manipulations may not always provide an accurate indication of genetic constraints on form, they do furnish a valuable test of hypothesized causal relations.

Fourth, the study of ontogeny is not without its difficulties and limitations. Embryos and larvae, as well as adults, have specializations and novel structural features. Ontogenetic trajectories of related species may diverge and then converge, confounding attempts to define general and special characters based on the order of appearance during development (Wake and Roth, this volume). In addition, cell dynamics during ontogeny may be complex and we should not necessarily expect that the first branchial arch, for example, will be derived from only one tissue source.

Analysis of Phylogenies

The analysis of phylogenetic patterns is basic both to the comparative analysis of structural systems and to the construction of explanations and descriptions of historical change (scenarios). Our view is that scenarios have heuristic value for integrating aspects of the biology of a clade and that many scenarios are testable.

Our discussions considered testable scenarios about the evolution of cichlid fishes in Africa (Liem 1973) and about the early evolution of vertebrates (Gans and Northcutt 1983). A testable scenario might, for example, involve a hypothesized key innovation for a clade and a hypothesized sequence of environmental changes that occurred during the evolution of a clade. In general, strong corroborative evidence for detailed scenarios is difficult to obtain, but scenarios are falsifiable using methods of phylogenetic analysis and comparison of clades in different environments. In order for scenarios to be maximally informative, they should incorporate information from a broad set of related taxa, not merely a subset of a clade, and should consider biology broadly, not restricting themselves to a single character or functional system.

Functional Analysis

We view the evaluation of both function and biological role in the feeding mechanism to be a critical task that is fundamental to our understanding of vertebrate diversification. A great deal of attention has been devoted to structural features, their description as characters, their use in phylogenetic analyses, and their developmental patterns. In contrast, functional aspects of feeding systems are still poorly known. Compared to the data base on structural systems, we have few detailed hypotheses of phylogenetic patterns to function and even fewer comparative analyses of function in a monophyletic clade. In part, this may be because the determination of muscle activity patterns, bone displacements, fluid pressures, or forces on the skeleton is difficult, expensive, and time-consuming. The rate of failure in laboratory experiments seems to rise exponentially with the addition of each technique to measure an additional functional parameter. To achieve a modest appreciation of function for even one structural complex in a monophyletic clade is a major task. The nature of integration and transformation in complex systems can only be appreciated if comparative *functional* analyses accompany structural description and the use of structures as characters.

Functional analysis, for example, may provide data on the "fundamental niche" of an organism (what an organism *can* do) while an accompanying ecological analysis is needed to determine the "realized niche" (what the organism actually does).

Deductive Methods: Predictions and Models

While the description of organismal function by the measuring of physiological parameters such as muscle activity and fluid pressures is clearly an important aspect of a research program in evolutionary morphology, we feel that biomechanical and biocybernetic models must be formulated quantitatively to allow prediction. These causal models describe the feeding mechanisms in terms of the *causa efficiens* and they allow predictions about certain form-function relations which need to be tested with real data. Apart from models of the feeding mechanism itself, we need models for the mechanisms underlying *change* in feeding systems. Such models of change are, of course, derived from inductive and comparative analyses. Models of the mechanistic bases of design not only need to be phrased verbally or qualitatively, they also need to be formulated in a quantitative or mathematical form (e.g., as a specific scaling factor or maximization function).

Once such causal models are available, it will be possible to generate theoretical transformations of the feeding system. Such transformational models mark a switch from inductive to deductive research as themes of change can be tested rigorously in specific case studies by deduction and

prediction (e.g., Zweekers 1979). Such models have the significant virtue of allowing manipulation of the components to produce a diversity of theoretical forms (a morphospace) that can be compared to realized biological designs. In certain systems, such as the avian feeding apparatus, explicit predictions of the likely direction of structural transformation may be possible by manipulating the model and calculating probabilities for the generation of specific morphotypes (Zweekers 1979). A deductive approach to feeding systems is a valuable adjunct to comparative and historical analyses of transformation in clades. It allows a rigorous testing of integration and hypotheses derived from comparative research.

COMMON THEMES UNDERLYING THE CHANGE AND INTEGRATION OF FEEDING SYSTEMS

In an effort to bring together many of the ideas that have been adduced as explanations for the modification of vertebrate feeding systems, we provide a brief discussion of twelve important factors that have been suggested as having played a role in the diversification of the trophic apparatus. Implicit in this list, but made explicit in our conclusions below, is that we believe a diversity of factors is involved in the transformation of feeding systems; no one mechanism explains all cases of structural modification.

Scaling

Innovations in feeding systems may appear as a result of scaling relationships as body size increases or decreases in a clade. The structural consequences of scaling effects may be quite dramatic, as exemplified by studies on miniaturization in salamanders (Hanken 1983; Roth and Wake 1985); novel arrangements of parts of the skull, brain, brain tissues, and sense organs may occur and proportional changes may have dramatic effects on feeding biomechanics.

Polymorphism

Trophic polymorphisms are of special interest because a single population displays both primitive and derived aspects of skull structure and function. These cases illustrate clearly that major alterations in skull design can appear and be maintained within a population (e.g., Meyer 1987). Within vertebrates, cases of trophic polymorphism are known in teleost fishes, salamanders, toads, turtles, and finches.

Plasticity

Phenotypic plasticity is common in the craniofacial skeleton and represents a change in structure and integration in response to use or dietary differences. While such changes could become heritable by genetic assimilation (*sensu* Waddington), the significance of phenotypic plasticity lies in the documented production of novel structural variants by the developmental system in response to environmental perturbation.

Decoupling of Parts

Decoupling of components (whether genetic, functional, or structural) in the feeding system provides a vehicle for the origin of novel features. We have noted that the availability of more than one structural system to perform a role releases primitive constraints and that a second, decoupled pathway may be modified in phylogeny to assume new structural and functional roles. We view decoupling as a permissive concept: structural diversification in a clade may require, in most cases, appropriate environmental opportunities. Examples of decoupling as a process permitting diversity are provided by feeding systems of fishes, salamanders and mammals, gene evolution, and neural pathways underlying electroreceptive function in teleost fishes (see also Roth and Wake, this volume).

Key Innovations or Novelities

While several of the topics discussed above could be viewed as providing "key" innovations (Mayr 1960; Liem 1973), this concept is usually reserved for a specific change which initiates a cascading effect of successive changes in a clade. Originally, the concept of a key innovation was causally related to speciation ("adaptive radiation"), but we wish to emphasize key innovations as novel features which, once acquired, allow structural or functional diversification in a lineage. Key innovations could be in genetic correlation structures, morphological, physiological, or behavioral features, and hypotheses about their historical effect can be tested using phylogenetic methods (Lauder 1981; Lauder and Liem, this volume). We view key innovations as having no necessary relation to speciation, but instead as being most informative as a historical hypothesis when an innovation is proposed to be related to structural and functional diversification in a monophyletic clade.

Accumulation of Small Changes

While relatively rapid alterations in design may occur after a key innovation appears, reorganization in feeding systems may also involve a series of small

changes, none of which constitutes a major structural novelty. The accumulated effect of the sequential changes, however, often generates novel feeding patterns and new biological roles for existing structures. One example of this phenomenon is the sequence of changes in the lower jaw and middle ear of early mammals. Reduction of postdentary bones, reorganization of jaw adductor musculature, and reduction of primitively large pterygoid muscles may all have permitted a new pattern of integration in the early mammalian jaw apparatus (Crompton, this volume).

Genetic Correlations

The pattern of genetic correlation may strongly influence how integration in feeding systems changes. A strong genetic correlation between traits may make it impossible to change one character without another, thus preventing significant diversification of traits. This is an area in need of considerable further investigation. There is evidence from Darwin's finches that very strong selection can produce morphological differentiation, even among traits that have high genetic correlations, without a reduction in the correlation among traits (Boag 1983; Grant 1986; Schluter 1984).

Excessive Construction

One factor that may allow a change in integration is that most individuals within populations have feeding systems able to deal with environmental demands greater than those currently present. Such excessive construction (Gans 1979) could allow individuals to take advantage of environmental opportunities and may be especially important in the invasion of new habitats.

Adequacy of Design

Given the extensive diversification in vertebrate feeding systems, there is a tendency to focus on the close matching of structure and function in many clades. Often overlooked is the possibility that novel patterns of skull integration need only be *adequate* for functional demands (Gans 1988a). Especially after patterns of integration in the head have changed, for example, by the introduction of new features, the function of a structural configuration need only be sufficient; increased efficiency will likely arise in descendant clades.

The Capacity to Use New Opportunities

The origin of structural novelties will have little historical effect unless a

opportunity. Many in the group felt that unless individuals in a population possess a range of behavioral plasticity broad enough to permit the invasion of new habitats if they open up, then structural, genetic, or functional novelties arising in that population are unlikely to be maintained or to spread. Often we see various ways in which environmental opportunities are met by several evolutionary solutions, providing "experimental radiations" (Gans 1989).

The Opening of New Ecological Opportunities

There is no doubt that an important factor underlying changes in integration of feeding systems is the opening of new habitats to species through accidental discovery, tectonic events, or range extensions during periods of climatic fluctuation. Such novel habitats provide a new constellation of selective forces on biological design and may permit the disruption of primitive genetic constraints and the alteration of structural configuration. Classical examples of radiation in the face of novel environmental opportunities include cichlid fishes and Darwin's finches.

Levels of Organization

The evolution of complex feeding systems may occur at one or more levels of organization. Variation among taxa within a clade in behavior, for example, may be due to changes in the topology of the musculoskeletal system, to changes in the physiological properties of jaw muscles, to changes in the motor pattern to jaw musculature, or to changes in central nervous system structure. How does integration change among these levels in ontogeny and phylogeny?

There are too few case studies to allow one to generalize about the frequency of change at any one of these levels, but many in the group felt that current data point toward a greater plasticity in peripheral morphology as compared to central nervous system design. Many features of the motor system in the brain, for example, are highly conserved across vertebrates despite major changes in peripheral musculoskeletal morphology (Roth and Wake; Székely and Matesz; and Crompton, all this volume). The design of sensory systems in the vertebrate brain appears to be less conservative. Despite the apparent conservatism in central motor organization, we still have little information on the comparative anatomy (and thus the extent of conservatism) of motor circuits and motor patterns output to jaw musculature.

MAJOR CONCLUSIONS

There are six major conclusions that emerged from our discussions on the

1. Not all complex subsystems within an organism are integrated and evolve in the same way. For example, we believe that the pattern of integration and evolution in the feeding mechanism is different from that of the locomotor apparatus in vertebrates.

We propose four basic reasons for the difference in integration between feeding and locomotor systems. First, we suggest that the locomotor apparatus and supporting cardiovascular tissues receive, on average, a higher fraction of the total organismal energy intake than feeding structures. Even rapid feeding behaviors require relatively little energy, and the muscles, bones, and sense organs associated with the feeding mechanism receive only a small fraction of cardiac output. This suggests that the design of feeding systems may be less restricted by specific environmental constraints on their design and function. For example, the high density and viscosity of water in comparison to air produces well-defined hydrodynamic constraints on the design of locomotor systems in fishes: there are only a few possible designs for efficient locomotion in water. Feeding systems, however, are not under such severe hydrodynamic constraints. Within a given clade of fishes, locomotor morphology may be quite similar among species, while feeding structures vary considerably.

Second, the interacting components of the feeding mechanism develop in a region demanding accommodation of the special influences of other cranial components and of several tissue sources. The vertebrate craniofacial system is of compound origin developmentally and this contrasts with the relatively uniform developmental basis of the locomotor apparatus. The increased constructional flexibility allowed by multiple (and conflicting) developmental pathways may explain why so many fundamentally different feeding designs have evolved within vertebrates (Gans 1988b). The feeding system also develops at the anterior end of the notochord near the major sense organs and neural tissues controlling organismal function.

Third, the skull of vertebrates is made up of many mechanical units and it was agreed that the primitive gnathostome feeding complex included a kinetic upper jaw coupled to other craniobranchial components: evolution of the jaw in all clades derived from this. Thus, many mechanical linkages involving numerous bones, muscles, and ligaments are present and allow considerable constructional flexibility. Flexibility of design appears to be an intrinsic feature of many vertebrate feeding systems.

Fourth, ecological interactions between species (predation, competition for food, etc.) provide an impetus for diversification in the feeding apparatus. The environment "faced" by the feeding apparatus consists of an array of prey species, sizes, and life stages that may greatly change on a daily, seasonal, and yearly basis. Thus, feeding may be intrinsically more variable in terms of the environmentally (and temporally) available food types.

One implication of this proposed difference between integration in feeding and locomotor systems is that the research methods for studying the two

systems will differ. Measurement of maximal performance and efficiency will be both easier and more meaningful in the locomotor apparatus, while the examination of alternative designs that solve a similar functional problem may be a more fruitful approach to feeding. This is not to say that it is always impossible or uninformative to measure feeding performance: this has been done, and with interesting results. Rather, our point is that *in general* the performance of locomotor systems is more easily assessed using maximal performance measures, and that this is a consequence of differences in integration between feeding and locomotor systems.

2. A major theme in vertebrate evolution is the diversification in feeding systems. More than any other complex structural system, the musculoskeletal and neurosensory components of the feeding mechanism show spectacular diversification and differentiation in vertebrate clades. We feel that this is due to the multiplicity of developmental mechanisms involved in generating the feeding system (thus providing many possibilities for altering developmental and functional integration) and to the opportunities offered by the multidimensional environmental space with its diversity of prey and habitat types.

3. We were impressed with the role of ontogeny in facilitating the innovation and continuing integration of structural systems. Ontogenetic analyses clearly reveal the extent to which large structural changes can be achieved by relatively minor alterations in developmental pathways. In addition, analyses of feeding systems through ontogeny demonstrate the extent to which many structural components and their interconnections can be altered while function and performance of the entire system is maintained.

4. We conclude that many of the dichotomous perspectives offered as alternative ways of studying complex systems can be falsified by empirical research programs (e.g., the importance of genetic versus epigenetic factors), while other dichotomies (e.g., structuralist/functionalist) are best used to achieve a synthetic and more heuristic explanatory framework.

5. We agree that one important general hypothesis to explain the diversity of complex structural systems is the decoupling of primitively constrained elements of integrated design (possibly involving the unlinking of developmental pathways, changes in genetic correlations, and change in mechanical linkages). We emphasize that such decoupling of components in a structural system must be associated with the capacity of species to take advantage of these opportunities and followed by appropriate environmental opportunities.

6. We find that no one general hypothesis explains the nature of integration and its transformation in the feeding mechanism. The lack of a single general explanation is due to (a) the complex developmental basis of head structures, (b) the relatively low portion of the organismal energy budget used by feeding structures and the consequent lack of tight performance constraints on alternative skull designs, (c) the role of novel environmental opportunities for ecological diversification, and (d) the complex, diverse, and changing

nature of other organisms available as prey (thus facilitating the evolution of alternative capture mechanisms).

FUTURE RESEARCH QUESTIONS AND DIRECTIONS

Our discussions on future research programs generated nine specific questions (listed below). We also wish to emphasize the importance of three general issues that form the basis for the suggested research questions. First, we agreed that form-function predictions can be made and that these predictions are testable. Second, we agreed that genealogical hypotheses form the basis for comparative analyses of organismal design and that hypothesis testing must involve monophyletic clades. Third, it is clear that our knowledge of the diversity of feeding systems in vertebrates is completely inadequate and must be greatly expanded in the context of future research programs; phylogenetic hypotheses represent an obvious basis for such comparisons.

1. Does structural or functional decoupling always imply decoupling of epigenetic pathways or correlations? We currently have no idea whether the uncoupling of biomechanical linkage systems, for example, is accompanied by a reduction in the genetic correlation between these biomechanical elements. This question could be addressed by examining a clade within which a mechanical decoupling in the feeding mechanism occurs. Using a phylogenetic hypothesis to define the hierarchical level of the biomechanical innovation, we could then conduct quantitative genetic analyses of the feeding mechanism by measuring characters in groups of parents and offspring from each of the terminal taxa. The patterns of genetic correlation could then be mapped onto the cladogram to test for congruence among genetic and biomechanical decouplings.

2. What is the developmental genetic basis of trophic polymorphisms? Is the variation heritable? Several vertebrate species show considerable polymorphism in the trophic apparatus and provide an exciting opportunity to study integration in feeding systems unencumbered by the difficulties inherent in interspecific comparisons. Breeding programs, quantitative genetic analyses, and feeding performance testing of polymorphic species will aid in understanding the origin of diversity in complex structural systems.

3. How do structural, functional, and genetic interactions in complex systems change during ontogeny? Several vertebrate clades offer excellent test cases. In teleost fishes and amphibians, functional, morphological, and scaling analyses of critical life history stages will clarify ontogenetic changes in integration of the feeding system. In addition, the timing of the development of functional complexes in the skull could be studied in lineages with differing life history strategies (e.g., oviparous or viviparous). Unless much more analysis of inductive systems and of functional and biomechanical requirements of craniogenesis in all clades is accomplished, we will be

critically limited in our understanding of many constraints on adult skull structure.

4. What is the relationship among changes in central nervous system design, motor output, peripheral morphology, and the genetic basis of these characters? Many vertebrate clades could be used to examine this general question. For example, one could study how the control of the feeding mechanism is modified in the ontogenetic transition from suckling to mastication in mammals or from the larval to the adult stage in amphibians. Or, one could investigate the brain, motor pattern of the jaw musculature, and musculoskeletal design in a monophyletic clade of birds to study the congruence among these characters.

5. What is the basis of intra- and interspecific variation in motor output from the central nervous system to the feeding musculature? We currently understand very little about the causal factors that produce variation in motor patterns. Particularly, informative analyses could be conducted on vertebrates that can feed in both water and land: this would clarify the constraints of the environment on feeding function. The process of metamorphosis in amphibians also provides exciting opportunities for testing the effect of morphological changes on motor patterns and for clarifying ontogenetic changes in motor pattern integration.

6. We need to introduce more quantifiable models of feeding mechanisms as well as quantitatively formulated mechanisms of change so that the application of deductive procedures will allow us to develop a diversity of tests of hypotheses of structural diversification within monophyletic clades.

7. How do environmental factors interact with epigenetic systems in generating phenotypic plasticity? We still understand little about the mechanisms causing the origin of novelties within developmental systems in the feeding mechanism.

8. How do structure and function in the feeding mechanism relate to organismal performance and fitness? While the performance of feeding systems can be difficult to quantify as noted above, several studies on fishes, salamanders, birds, and mammals have successfully accomplished this task. We need to extend this approach to other taxa and to examine explicitly the limits to feeding performance for comparison to locomotor systems. In order to test the hypothesis that feeding and locomotor systems differ in their constructional flexibility and in their interactions with the environment, we need quantitative analyses of the performance of both systems within a monophyletic clade.

9. What is the relationship between the acquisition of key innovations promoting diversification in feeding structures and speciation rate? While great care has been taken to separate out speciation from structural analyses of innovations, we have little information on the relationship between changes in trophic design and speciation rate. Is there a causal relationship

between alterations in trophic design and subsequent speciation within a clade?

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