

Conservatism and Innovation in the Evolution of Feeding in Vertebrates

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Abstract. Processes that modify ontogenies can have profound morphological consequences. Heterochrony is one means by which ontogenetic pathways can be changed to give large morphological changes in adults of related taxa with relatively little genetic change. On the one hand, developmental interactions during development are so complexly integrated that they provide a stability to the characteristic morphology of lineages and give the impression of recapitulatory evolution. On the other hand, when the opportunities for modification of ontogenies arise, the results can be dramatic. Repatterning of ontogeny may be an important means by which evolutionary novelties are introduced. Both structuralist and functionalist perspectives, within a phylogenetic framework, contribute importantly to the understanding on the role of ontogenetic changes in the evolution of complex, integrated systems in vertebrates.

INTRODUCTION

Organismal unity, required for the performance of many tasks, arises from the interconnection of subsystems resulting from various kinds of connections or couplings (Table 1). Because such couplings exist, the evolutionary fate of different subsystems often is determined by that of others. Conservatism in one subsystem may lead to conservatism in others; conversely, significant change in one subsystem might lead to concomitant change in others as an outcome of internal dynamics and self-regulation of the system as a whole.

Phenomena affecting organisms as whole entities, such as the nature of the life history, can strongly affect certain subsystems and lead to evolutionary change in only certain directions. Ontogenetic shifts (e.g., metamorphosis) often involve major changes in habitat requirements (e.g., water to land).

TABLE 1 Kinds of couplings important in complex integrated systems.

I. <i>Genetic</i>
A. Pleiotropic and epistatic effects
B. Traits that are genetically correlated
II. <i>Ontogenetic</i>
A. Causal developmental linkage (e.g., induction)
B. Canalization effects
C. Phylogenetically conserved ontogenetic trajectories
III. <i>Structural</i>
A. Material
B. Mechanical
IV. <i>Functional</i>
A. Physiological
1. Single system (tongue use for apprehension and transport of food, as well as in deglutition and speech)
2. Multiple system (e.g., swimming and gill ventilation, running and breathing, feeding and breathing)
B. Integrative
1. Neurological
2. Endocrinological
C. Behavioral

which in turn require different kinds of integration at different points in the life of an individual organism.

Both internal and external factors are important in the evolution of complex integrated systems. Internal factors such as generative rules of development determine the kinds of morphologies that appear, but the morphologies must be inherited and must function in the real world. Networks of interacting constraints (as in morphogenetic processes) can both limit and orient qualitative and quantitative aspects of morphological adaptation and specialization.

Given these and related phenomena, which would appear to have a conservative influence, a major problem in evolutionary biology is: how are evolutionary novelties introduced into coupled systems? In this paper we examine this question from the perspective of the evolution of feeding mechanisms in vertebrates.

In the past, reconstruction of events in the evolution of functional systems often proceeded without benefit of an independent phylogenetic hypothesis, and the "morphoclines" that resulted from the morphological analysis were interpreted as if the phylogeny could be read directly from the morphology. We emphasize the need of a rigorous analysis of the morphological data within an historical framework (Lauder 1981; Liem and Wake 1985).

MORPHOLOGICAL AND NEUROLOGICAL BASES FOR FEEDING BEHAVIOR IN VERTEBRATES

Components of Feeding Systems in Vertebrates

General aspects of the functional and comparative morphology of feeding are known for most groups of vertebrates (Bramble and Wake 1985; Lauder 1985a; Hiiemae and Crompton 1985). Introduction of novelties differs greatly in aquatic and terrestrial environments, which we treat separately.

Aquatic feeding. Inertial suction feeding with unidirectional water flow is thought to be the ancestral feeding mode for active gnathostomes. In this mode jaws are mainly hoops which keep the mouth from collapsing and which direct water flow as buccopharyngeal expansion creates negative pressure. The hyobranchial apparatus, controlled by brainstem motor nuclei, plays crucial roles in this feeding mode. The highly consistent anteroposterior sequence of cranial expansion is important in mediating nonsteady water flow during suction feeding (Lauder 1985a). The relation of this pattern to the pattern of organization and generation of neural control has not been investigated.

Bemis and Lauder (1986) outline four major aspects of aquatic feeding (see also Lauder 1980, 1985a, 1985b) that were primitive not only for teleostome fishes but, because they are found in the lungfish *Lepidosiren* (lungfishes may be the sister group of tetrapods), also for tetrapods. These are (a) prey capture by means of unidirectional-flow suction feeding; (b) mouth opening associated with cranial elevation accomplished by contraction of epaxial muscles; (c) expansion of the buccopharyngeal cavity and depression of the mandible accomplished in part by the hyobranchial apparatus; (d) peak hyoid excursion occurring after the achievement of maximal gape. Yet, this conservative pattern has not limited the diversity of behavior and performance to any great degree. As Liem (1984a) has pointed out, prey capture techniques among suction feeders are inherently versatile, determined by the medium and governed by hydrodynamic principles. Liem provides examples of single species that can capture and consume a great variety of food. The neuromuscular programs of fishes are diverse and greatly exceed those of tetrapods in number and versatility. (Liem [1984a] refers to a rich repertoire of "software" governing feeding actions of fishes.)

Terrestrial feeding. Terrestrial tetrapods have a more stereotyped feeding system than do aquatic vertebrates. As in fishes, the brainstem continues

to play the critical role in coordination (brainstem organization is generally conserved throughout gnathostome evolution). The hyolingual system of tetrapods, derived from the fish hyobranchial system, is critically important in terrestrial feeding, both in apprehension and transport of food. Specialization of hyolingual systems leads to novel feeding modes in many terrestrial groups (Bramble and Wake 1985). Mastication is especially important in mammals, and it is accompanied by the development of specialized muscles and dentition; yet, the basic feeding mechanism is so similar among all mammals that a common neural control system is implicated (Hiimae and Crompton 1985; Crompton, this volume).

Bramble and Wake (1985) argued that the structural and functional organization of terrestrial tetrapod feeding complexes manifests a general pattern associated with the water-land transition. Biophysical constraints associated with feeding in air (as contrasted with water) relate mainly to differences in density and viscosity and require substantially different ground plans for function; there is a great conservatism in food transport during ingestion, intraoral transport, and deglutition. Tongue use is common in terrestrial feeding, and it is lingual transport that most sharply distinguishes terrestrial from aquatic feeding in vertebrates.

A model for a generalized feeding cycle in terrestrial vertebrates hypothesizes a rhythmic intraoral transport cycle involving ingestion, mechanical reduction (if present), and transport of food through the oral cavity to the esophagus (Bramble and Wake 1985). The model involves a ratchet-like mechanism composed of successive strokes. Certain motor events are so rapid and stereotyped as to suggest a central neural preprogramming within the brainstem motor column. The cycles of movement of the hyoid apparatus and of the tongue surface in mammals, and the pattern of their linkage to the jaw-movement cycle, led to the suggestion (Hiimae and Crompton 1985) that tongue-movement cycles are critical components of the complex feeding system (Crompton, this volume).

In contrasting terrestrial vertebrates with aquatic feeding of fishes, Liem (1984a) has commented that tetrapods rely on a very restricted neuromuscular "software," while jaws, teeth, skulls, and muscles have evolved as specialization proceeded (for example, specialization in mammals is based on differentiation of muscles and teeth [Lund and Enomoto 1988]). This has led to the evolution of much higher degrees of feeding specialization (by which we mean restriction in diet in terms of taxa, size, quality, etc.) in tetrapods than seen in fishes. Perhaps this specialization arises as an evolutionary consequence of the relative constancy of the preprogrammed oscillations and jaw movements found in tetrapods (Liem 1984a). This example shows that a constraint at one level can lead to evolutionary diversification at other levels of organization within a major lineage.

THE EVOLUTION OF COUPLINGS

Although structural and functional couplings have been discussed at length (e.g., Dullemeijer 1974; Gans 1974), little is known about their establishment. Lauder (1981) has argued that, within a clade, systems are often constrained by couplings; functional, structural, or morphogenetic networks will have a greater number of independent systems (his "decoupling hypothesis") in more speciose than in less speciose lineages.

THE INTRODUCTION OF EVOLUTIONARY NOVELTIES INTO COUPLED SYSTEMS

Features that permit a rapid departure of a group of organisms from a preceding ecological sphere are called key innovations (Liem 1973; Larson et al. 1981). In the following sections we focus on novelties and key innovations in a framework of couplings that might be perceived as constraints on evolution. We will see that such innovations can enter systems of couplings in many ways.

Structurally Coupled Systems That Have Different Functions

Feeding and breathing in fishes. Suction feeding is the dominant and primitive feeding mode in fishes, and it simultaneously acts to ventilate the gills, which lie within the opercular cavity. Four phases of prey capture can be recognized, based on timing of the movements of cranial elements: preparatory, expansive, compressive, and recovery (Lauder 1985a). These in turn are governed by musculoskeletal couplings, two of which have received considerable attention: levator-operculi coupling (perhaps a key evolutionary innovation [Liem 1980a]), based on a four-bar linkage system (Anker 1974; Barel et al. 1975, 1977), and sternohyoideus coupling (Liem 1980c). These two couplings cannot be mechanically optimized simultaneously because of biomechanical constraints (Liem 1980c). Sternohyoideus coupling alone can depress the mandible, but the apparently later addition of the levator-operculi coupling for mouth opening had many, far-reaching consequences. Most importantly, addition of this subsystem freed the sternohyoideus subsystem, enabling it to evolve new functions that enhance suction and food preparation. For example, the sternohyoideus coupling plays an active role in mastication by the novel pharyngeal jaws. The gills and gill arches come to play the role of a resistant element in the mouth cavity with important implications for feeding, while retaining their respiratory role. The branchial apparatus of ray-finned fishes functionally segregates the mouth cavity into two distinct areas with different functional characteristics (Lauder 1985a). The apparatus plays a crucial role in feeding

by decoupling events in the opercular cavity from those in the buccal cavity. As a partial consequence, the operculum comes to function less for the generation of suction than for the regulation of water flow. Thus, the apparently constraining effects of coupling at subsystem levels contribute to the appearance of an evolutionary novelty at another organizational level in a complex part-whole relationship.

The structural coupling of feeding and respiratory systems is seen in a dramatic way in air-breathing fishes (Liem 1980c). Many of the structural elements of air ventilation also play important roles in feeding in these fishes. What appears to be a drastic change in function, air breathing, is really the assumption of a new function by an existing functional complex without loss of other functions. Anabantoid fishes are characterized by a triphasic pattern of breathing that is virtually indistinguishable from the feeding cycle. Other air-breathing fishes have a quadruphasic pattern that is very similar to the "cough" patterns. An air bubble replaces a prey item in triphasic breathing, and what was gill-cleaning activity becomes in quadruphasic breathing the flushing out and then sucking in of an air bubble. Anabantoids have a relative high degree of feeding specialization, and they have become very effective air breathers. In contrast, synbranchiform and channiform fishes, which lose air while feeding, have unspecialized feeding mechanisms but highly specialized breathing mechanisms. Thus, a complex coupling between feeding and respiratory functions at the structural level might have prevented optimization of both in these groups (Liem 1980a, 1984b, 1987).

Feeding and breathing in frogs and salamanders. Frogs and salamanders differ dramatically in feeding and breathing, yet structural mechanisms serving both functions are coupled directly, and the same basic structural components are found.

Salamander larvae have external gills, supported by articulated gill arches which are moved by a relatively complex musculature. Gill waving occurs in an anterior-to-posterior sequence. There are strong similarities between unidirectional suction feeding in fishes and in salamanders (Lauder 1985a; Lauder and Shaffer 1985, 1986). The functional similarities are reflected in structural similarities, especially in the hyobranchial apparatus, and in both fishes and larval salamanders feeding and respiration are accomplished by the same acts, although gill-waving can proceed independently of feeding.

Gills of frog larvae are covered by opercular skin and they are not waved. Rather, they are irrigated by water flow that is part of the feeding act in some species (e.g., the suspension feeding *Xenopus* [Wassersug 1980]) but have various degrees of independence from feeding in others (e.g., those species that have scraping mouth parts). A characteristic of tadpoles is a basket, formed by a melding together of elements of the hyobranchial

apparatus, that works in concert with the large ceratohyals, which in turn form the "piston" portion of a buccal pump.

Metamorphosis is relatively modest in salamanders, and structural changes in the jaws and hyobranchial apparatus are not extensive. The hyobranchial apparatus becomes a hyolingual system with the appearance of a tongue pad. Lateral parts of larval gill arches show an anterior-to-posterior size gradient, which is retained as the branchial arches metamorphose into tongue skeletal elements; thus, the first ceratobranchial is larger than the second and is the dominant force-transmitting element from the protractor muscle to the tongue pad (Wake 1982a). The hyolingual apparatus moves forward in relation to the relatively fixed ceratohyal elements by means of contraction of a modified branchial muscle, the subarcualis rectus I. Posteroventral movement of the hyolingual apparatus induces abduction of the mandible by means of the mandibulohyoid ligament. This coupling also is found in lungfishes (Bemis and Lauder 1986). We conclude that this coupling is a retained primitive trait in salamanders (critical information is unavailable for *Latimeria*). Despite this relative conservatism in structure and ontogeny, lunged salamanders are able to accomplish a moderate degree of hyolingual projection. Because the hyolingual system is also a force pump which fills the lungs, the amount of tongue projection is limited by the coupling of respiration and feeding in this system (Wake 1982a). Thus, the conflicting functional requirements of ventilation and feeding restrict further specialization for tongue projection.

The lungless salamanders (Plethodontidae) have evolved extreme specialization in regard to tongue projection, based on an elaboration of the posterior parts of the hyolingual apparatus. The epibranchials have become greatly elongated, and they are surrounded by spirally wound subarcualis muscles (Lombard and Wake 1976, 1977). The hyolingual apparatus has been freed of the constraints associated with respiration, and optimization of mechanics associated with feeding has occurred. This extreme specialization with regard to precision, distance, and velocity of prey capture (reviewed in Roth 1987) occurs within the framework of the conservative tetrapod feeding system.

Metamorphosis is profound in frogs as compared with salamanders. During metamorphosis, the condensation and fusing of the parts of the hyobranchial apparatus proceeds. The distal epibranchials disappear. This results in a simplified hyoid plate with fused ceratohyals (de Jongh 1968). Ligaments attach the extreme distal tips of the ceratohyals to the skull. Muscles involved in major movements of the hyobranchial apparatus of larvae either disappear (subarcualis rectus and rectus obliquus muscles) or transform into petrohyoideus muscles that have orientations at right angles to the orientation of muscles served by the same nerve that protract the tongue in salamanders. These petrohyoideus muscles have no feeding function, but serve in

respiration and vocalization. The petrohyoideus series, together with some other muscles (especially the omohyoideus series), are major components of the buccal force pump that fills the lungs in frogs (de Jongh and Gans 1969; Gans 1974).

Ventilation in frogs is more elaborate than in salamanders. Further complicating the respiratory functions is the sound production system of frogs, the anatomical basis of which is equivalent to ventilation but with some important extensions (body muscles are also involved, a vocal sac is present which may be partly inflated during the call, and the larynx serves not only as a valve between the buccal cavity and lungs but also as the producer of vocalization [Gans 1974]). The pulse-pumping ventilation system is considered to be relatively inefficient, but it has advantages for sound production (Gans 1974). The larynx of frogs is intimately coupled to parts of the unified hyoid plate which is the outcome of the condensation and reorganization of the hyobranchial skeleton during metamorphosis. Thus, the hyolingual apparatus of adult frogs is deeply compromised by several important functions that constrain its use as a component of lingual feeding. Yet, frogs use very effective and far-reaching lingual projection for prey capture. Whereas in salamanders with highly specialized tongue projection a part of the hyolingual skeleton bearing the tongue pad is launched from the mouth, in frogs there is a completely different system. The general pattern in frogs involves no hyoid movement. Instead, a unique arrangement of hyoglossal and genioglossal muscles in the tongue pad, and submentalis and geniohyoideus muscles in the floor of the mouth, interacts to accomplish tongue protraction. The tongue pad muscles stiffen to form a ballista which is tipped over a rising fulcrum formed by the muscles in the anterior floor of the mouth (Gans and Gorniak 1982).

Corresponding to the differences in functional morphology outlined above, different nerves and motor nuclei of the brainstem and cervical spinal cord are involved. In salamanders, tongue protraction is under the control of the ninth and tenth nerves, and retraction is controlled by the first (hypoglossal) and second spinal nerves (Roth and Wake 1985a). In frogs, both protraction and retraction are controlled by the hypoglossal nerve, in interaction with other muscles served by the fifth nerve. The hyobranchial apparatus of frogs has been so extensively remodeled that the ninth and tenth motor nuclei play no role in motor control of the tongue for prey capture (Gans and Gorniak 1982). The result is a convergence of frogs and salamanders, and even among different taxa of salamanders, on a common end result, i.e., protraction of the tongue for a relatively great distance to apprehend prey.

Functionally Coupled Systems That Have Different Structures

An example of innovation resulting from the functional coupling of novel structures also involves the breaking of a functional constraint by uncoupling.

Generalized perchlike fishes (e.g., centrarchids) have a pharyngeal jaw apparatus which has a limited functional repertoire for processing and masticating food, and this, in turn, appears to have an inhibiting influence on the diversification of the mandibular jaws, which act in prey capture. Both the pharyngeal and mandibular jaws remain functionally and morphologically conserved in generalized percoid fishes (Liem 1980a). In labrid and cichlid fishes, the pharyngeal jaw apparatus becomes suspended in a muscle sling (Liem 1973; Liem and Sanderson 1986), conveying a wide range of functional capacities in processing prey, thereby freeing the mandibular jaws to evolve into highly efficient prey-capture devices. The uncoupling of the premaxillary-maxillary-suspensorial complex and the evolution of a complexly integrated pharyngeal-jaw apparatus is hypothesized to have triggered a spectacular diversification in the feeding apparatus of cichlids (Liem 1980b; Liem and Sanderson 1986). A combined functional and historical analysis suggests a direct relationship between these changes in functional coupling and the great increase in ecological and morphological diversity.

Gans (1974) has vividly shown how novel structures in egg-eating snakes (e.g., specialized intermediate vertebrae that crack the egg) can be coupled functionally and behaviorally to produce a cascading set of adaptive features. These include reduced cranial kinesis, bracing of supralabial scales to the marginal bones of the skull, and hypertrophy of the Harderian glands to provide a special lubricant. New couplings functionally related to feeding establish the foundation for new behaviors quite unrelated to the original adaptation. Thus, reduction of jaws and teeth, especially fangs associated with poison glands, is associated with a shift of diet and the removal of selection pressures for ancestral patterns of food procurement.

Functionally and Structurally Coupled Systems That Have Different Ontogenies

In plethodontid salamanders that retain larval development, metamorphosis is typically modest, and the basic arrangement of the branchial arches is carried over from larvae into adults. This arrangement features an anterior-to-posterior gradient of development, with anterior elements being relatively larger. Thus, as expected the first ceratobranchials are the larger of the two pairs, and they are the major force-transmitting elements (Lombard and Wake 1977). However, this arrangement imposes a constraint on the evolution of the system: although a high degree of hyolingual projection is possible relative to other salamanders, the system does not attain the extremes of specialization found in the bolitoglossine plethodontids. All members of the tribes Plethodontini and the Bolitoglossini have abandoned the aquatic larval stage. The bolitoglossines have the most highly specialized system of hyolingual projection, with the longest reaching, fastest, and most

versatile tongues (in terms of directionality). Direct development is a necessary, but not sufficient, step in this direction (members of the *Plethodontini* remain relatively unspecialized) (Roth and Wake 1985b). There has been an ontogenetic repatterning (see Wake and Roth, this volume), and the second ceratobranchial has become the force-transmitting member. This rearrangement has facilitated a phylogenetic "escape" from ancient functional and/or design constraints by a decoupling of structure and function during ontogeny.

Structural and Functional Systems That Become Decoupled

A phylogenetic analysis of the evolutionary morphology of feeding mechanisms in loricarioid catfishes has tested the decoupling hypothesis (Schaefer and Lauder 1986). An increase was found in the number of biomechanical pathways related to feeding in comparison with outgroup taxa. Decouplings of primitively constrained systems (e.g., mobility of the lower jaw symphysis) as well as increases in the number of biomechanical linkage systems were found.

Despite the apparent conservatism of tetrapod feeding, there have been some major divergences in different groups. The scleroglossan squamates (including all lizards, except iguanians, and all snakes) provide one example. Lingual transport has become decoupled from the remainder of the feeding system in these organisms, which use jaws exclusively in prehension (Schwenk 1987); accordingly, they have broken an important coupling in the general model of tetrapod feeding (Bramble and Wake 1985). The tongue of scleroglossans has become converted largely into a sense organ, although it is used in specialized ways for feeding (e.g., lapping liquids); this group has kinetic skulls, and kinesis may enable more efficient apprehension of food by jaws in the absence of tongue use (Schwenk 1987). Both the speed and force of the strike are improved by kinesis in varanid scleroglossans, and the mechanical advantage of the bite and size of the foodway are increased in relation to the akinetic iguanians (Condon 1987). Cranial kinesis associated with food transport reaches extreme degrees of specialization in snakes (Cundall 1983; Gans 1974; Greene 1988). Tooth-bearing bones in both upper and lower jaws have high mobility and are connected to each other and to the braincase only by ligaments and muscles. However, freeing of the jaws has had another important consequence, for food transport in the highly derived colubroid snakes has led to a shifting of the food-transport function from the maxillary to the more medial pterygoid bones. This uncoupling of structure and function has led to a truly radical innovation: the use of the maxillary bone in prey capture and the parallel evolution of venom-injecting specializations (Cundall and Greene 1982). Thus, in scleroglossans we see a confirmation of the predictions of the decoupling

hypothesis (Lauder 1981; Schaefer and Lauder 1986) at successive cladistic levels.

Structural and Functional Novelties Incorporated into Apparently Tightly Coupled Systems

Nonhomologous depressor mandibulae muscles that are active in mouth opening have been added convergently into the feeding system by lungfishes and tetrapods (Bemis and Lauder 1986). In lungfishes, tooth plates are present and food is manipulated and chewed. Hydraulic transport of food within the oral cavity is accomplished by movements of the hyobranchial apparatus in a manner very similar to the movement of food by the tongues of tetrapods.

Caecilians are limbless vertebrates which usually have compact skulls, and their feeding system probably evolved in the context of burrowing, in which a premium is placed on a smooth head of relatively small diameter. They display several departures from the generalized feeding system of tetrapods. In addition, they have co-opted a seventh-nerve muscle, the interhyoideus, which normally is a throat constrictor, to become a jaw adductor by its dorsoposterior migration along the body wall and its insertion (near its historical origin) on the greatly enlarged retroarticular process of the lower jaw (Bemis et al. 1983).

Iguanian lizards have the most generalized feeding systems in squamates. Yet, within the iguanians there has been a spectacular specialization in the projectile tongues of chamaeleons (Altevogt and Altevogt 1954; Bell 1984; Bels and Baltus 1987). An unusual ring muscle acts as the accelerator of the tongue. This muscle has been found in a less specialized state in the sister group of chamaeleons, the agamids (Schwenk 1984; Smith 1987), and some agamids show an intermediate behavioral stage which appears to foretell the chamaeleon condition (Schwenk and Bell 1988). The general model of kinematics for tetrapods (Bramble and Wake 1985) has been but slightly modified, and the cyclical movements of the jaws and hyolingual complex follow the generalized profile in most regards (Bels and Baltus 1987).

Food transport in birds takes place as a result of a scraper mechanism which is intimately integrated with the laryngeal mechanism that closes the trachea (aspects of the complex feeding system in birds are reviewed in Zweers 1985a). The novel avian organ, the syrinx, located at the lower end of the trachea, is responsible for sound production. However, differences in vocal performance appear to have arisen in part as a result of changes in food-transport mechanisms between ancestral and derived lineages. The larynx has evolved a new role in glissando whistling and increased duration of song, which in turn contributed to the development of a drill-chuck

laryngeal mechanism. This laryngeal structure represents a precondition for the evolution of a pharyngeal scraper system in passerines (Zweers et al. 1981; Zweers 1985a). The highly derived passerine larynx has an extraordinary morphology that can serve a role in vocal performance analogous to the cheeks and lips during whistling in humans (Zweers 1985a).

From a human perspective, perhaps the most spectacular innovation of the feeding system is the evolution of human speech, in which movements of the tongue and the hyolingual complex play critical roles. Yet, the hyolingual complex retains its generalized function in the feeding system (Hiimae and Crompton 1985).

CONCLUSIONS AND SUMMARY

We have emphasized empirical results and their significance for understanding how complex integrated systems evolve. In a short chapter it is impossible to consider methods of analysis and broader conceptual issues. These have been the subject of detailed treatment in recent years (Dullemeijer 1974, 1980, 1985; Zweers 1985b; Liem and Wake 1985; Lauder 1981; Wake 1982b; Wake and Larson 1987).

We have given a number of examples illustrating how novelties related to the feeding system in vertebrates have arisen within the context of existing functional and structural couplings. Under some circumstances novelties have been introduced without decoupling, but more frequently some functional or structural decoupling has proven necessary. This may occur, incidentally, as decouplings occur for extraneous reasons, opening new opportunities for change. Major novelties accompany dramatic changes in habitat (e.g., water to land), and we have explored the ways in which ontogenetic decouplings associated with such shifts can offer opportunities for evolutionary change. By focusing attention on couplings of various kinds we have attempted to show both how integrated systems evolve as wholes and how, at the same time, the parts of such systems can evolve with varying degrees of independence. Most of the work we have cited has been performed by functional morphologists who have worked in an atmosphere of avowed neodarwinist functionalism, in which the organisms are envisioned as responding to problems posed by the environment by natural selection, and are thus adapting. And yet, there has been a general unease with the idea that causal forces responsible for the evolution of complex systems reside exclusively at the genic and population level. The relation of parts and wholes, transformation of systems, and self-regulation are important components of structuralist analysis, and we believe that such an approach, conducted in a framework in which explicit recognition is given to historical (phylogenetic) factors, can be complementary to an approach based on genic and population-level functionalism (Wake and

Larson 1987). An important focus of a multidimensional approach is to determine why biases occur in evolution and why some kinds of changes are more likely than others. There has been a tendency in the recent literature to focus on "developmental constraints." Additional perspectives are offered by examination of systems of coupling in order to determine whether change is more likely to occur in some ways than in others. This chapter is an attempt to direct attention to this perspective.

Acknowledgements. We have benefited from discussions with D. Bramble, G. Lauder, K. Liem, K. Nishikawa, K. Schwenk, and M. Wake. The manuscript benefited from comments by K. de Queiroz, A. Larson, K. Liem, K. Nishikawa, and M. Wake. Research in the Roth laboratory is supported by the Deutsche Forschungsgemeinschaft and that in the Wake laboratory by the National Science Foundation.

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