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The application of functional morphology to evolutionary studies

Frietson Galis

According to D'Arcy Thompson¹ 'We rise from the conception of form to an understanding of the forces which gave rise to it'. Thompson's view about how morphology should be studied has gained importance again after a long period during which functional morphologists mainly studied the relationship between form and function in organisms as they are, or as they were supposed to be before they were fossilized. The study of the transformation of form and function and of the relationship between them provides important information for evolutionary biologists. Although there is, in practice, considerable overlap, these contributions to evolutionary studies can be conveniently divided into those that contribute to the understanding of evolutionary patterns and those that further the understanding of evolutionary processes.

Studies of functional morphology contribute in several ways to the understanding of evolutionary patterns and processes. The former include the unravelling of dependencies of characters and the construction of biomechanically feasible transformation schemes. Among the latter are the identification of structural novelties that facilitate a cascade of diverse structural changes, and the identification of mechanisms that enable the incorporation of evolutionary novelties into the integrated organism. The study of mechanisms that maintain the match between form and function during evolutionary (and developmental) changes is a new and important area for evolutionary biologists.

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a pair of antagonistic muscles is much higher than in two muscles belonging to different functional systems. Arguably, the changes in both antagonistic muscles should be counted only once and, at the least, such information should be judged differently in order to avoid overestimating the importance of a character³. The example of two antagonistic muscles is intuitively simple, but not all relationships between characters are so easy to infer, and careful functional morphological analyses are necessary to unravel the interdependencies. It is in this area that functional morphology can contribute to the construction of more-reliable phylogenetic trees.

An instructive example of the unravelling of seemingly unrelated characters is Bramble's⁴ study of a character complex involved with saltatory running in hares (*Lagomorpha*). Hares have a joint in their cranium that serves as a shock absorber during saltatory running⁴.

When the hare hits the ground, the presence of the joint causes the heavy anterior part of the head to fall against the stabilized posterior part (Fig. 1), forcing away intercranial blood. Both the relative displacement of the anterior part of the head and resistance offered against blood flow provide shock absorption. For continued shock absorption, the

Evolutionary patterns

Character interdependence and transformation

Phylogenetic trees are constructed on the basis of shared derived characters². It is important to know whether characters are interdependent and have evolved as a complex (e.g. a functional complex), or whether they are relatively independent³. For instance, the likelihood of changes in each of

original position of the anterior part must be quickly restored, which probably happens by a pulling force of the long and heavy ears (comprising one third of the weight of the entire head!) when they are in an upright position. As soon as a hare starts saltatory running, the ears flip upright and continue to be in that position as long as the running lasts. The unravelling of this character complex (including more obvious characters of the legs) has provided hypotheses about the evolutionary history of the Lagomorpha, that is, that some burrowing hares have evolved from running hares⁴.

A somewhat different approach that can significantly contribute to phylogenetic studies is the analysis of couplings between different functional systems. For example, there is a heated debate about whether microbats and megabats are mono- or diphyetic (largely summarized in Pettigrew⁵ versus Baker *et al.*⁶; Fig. 2). Arguments for monophyly are based on the presence in both micro- and megabats of suites of characters, including the wings, cranial vascular features and foetal membranes⁶. Arguments for diphyly are differences between the two groups in characters of several independent brain systems, the external genitalia, a forelimb character and the absence in megabats of sophisticated echolocation. Megabats uniquely share these different characters with primates and (as far as known) with dermopterans⁵. In addition, there are fossils of highly derived microbats that already used echolocation, pre-dating fossils of primitive megabats⁵. Molecular analyses have been inconclusive (e.g. Ammerman and Hillis⁷ versus Schreiber *et al.*⁸). In this controversy, a functional morphological analysis that not only addresses separate characters but unravels couplings between systems provides important insight^{9,10}, that has not received sufficient attention. In microbats there is a biomechanical and physiological coupling between echolocation, respiration and flight⁹⁻¹¹. This coupling permits echolocation with little extra energetic cost to flying, whereas echolocation without flying is costly⁹⁻¹¹. Echolocation pulses in flight are emitted during the end of the upstroke when concentrated air is expelled from the lungs and the greatest muscular force occurs to pull the wings downward⁹. The linked optimization of locomotory and sensory performance during the evolution of microbats suggests that the absence of sophisticated echolocation in megabats can best be explained by the independent evolution of this group^{10,11}. Thus, this functional morphological analysis supports the claim that megabats evolved from primates some time after microbats had become established, when primates already possessed a well-developed vision⁵.

Ideally, a functional morphological study provides information about the interdependency of characters, and also a transformation scheme of characters that is biomechanically feasible¹²⁻¹⁴. Such a transformation scheme, which does more than merely provide a functional interpretation of successive structural stages, yields information about the likely order of character changes. While such studies unfortunately remain rare, an example that provides such a biomechanically feasible transformation scheme was performed by Lombard and Wake¹² on plethodontid salamanders. They propose that the tongue changed from being attached and protrusile, via attached and projectile, to free and projectile. This scheme results in a cladogram that is not the most parsimonious (at least, if the difficulty of mechanical transformations is not included in the assumptions) but that is the most likely from a biomechanical perspective. In the most parsimonious scenario, a free and projectile tongue would have evolved on two occasions directly from an attached and protrusile one.

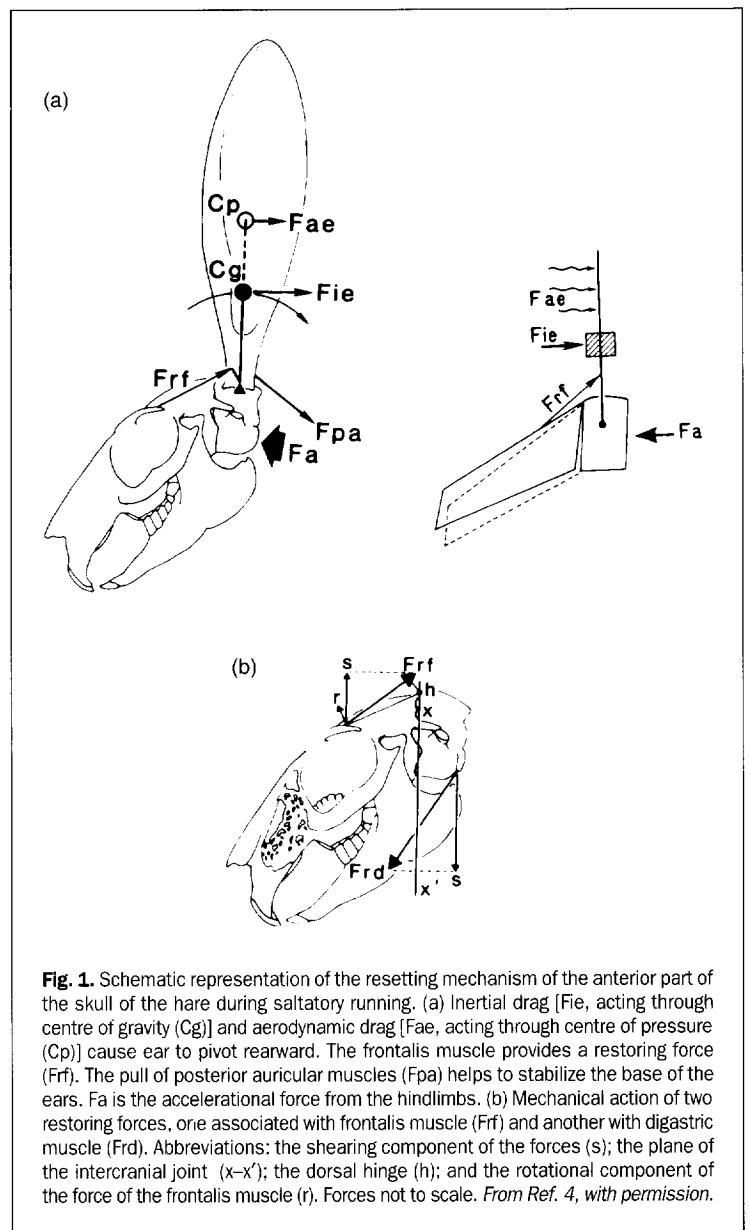


Fig. 1. Schematic representation of the resetting mechanism of the anterior part of the skull of the hare during saltatory running. (a) Inertial drag [Fie, acting through centre of gravity (Cg)] and aerodynamic drag [Fae, acting through centre of pressure (Cp)] cause ear to pivot rearward. The frontalis muscle provides a restoring force (Frf). The pull of posterior auricular muscles (Fpa) helps to stabilize the base of the ears. Fa is the accelerational force from the hindlimbs. (b) Mechanical action of two restoring forces, one associated with frontalis muscle (Frf) and another with digastric muscle (Frd). Abbreviations: the shearing component of the forces (s); the plane of the intercranial joint (x-x'); the dorsal hinge (h); and the rotational component of the force of the frontalis muscle (r). Forces not to scale. From Ref. 4, with permission.

Another example is a recent functional morphological study on a primitive alethinophidian snake, *Cylindrophis ruffus*¹⁵. Cundall¹⁵ argues that snakes are derived from (fossorial) scleroglossan lizards, with *Cylindrophis*-like snakes taking an intermediate position between lizards and advanced snakes. Braincase enclosure is supposed to be adaptive for a burrowing lifestyle and this characteristic of snakes, like limblessness, is most closely approached by fossorial lizards. Previously, however, a sturdy braincase and the increased mobility of some elements characteristic of snake skulls were seen as conflicting demands and thus as evidence against a fossorial ancestry (e.g. Ref. 16). According to Cundall¹⁵, structural changes in *Cylindrophis*

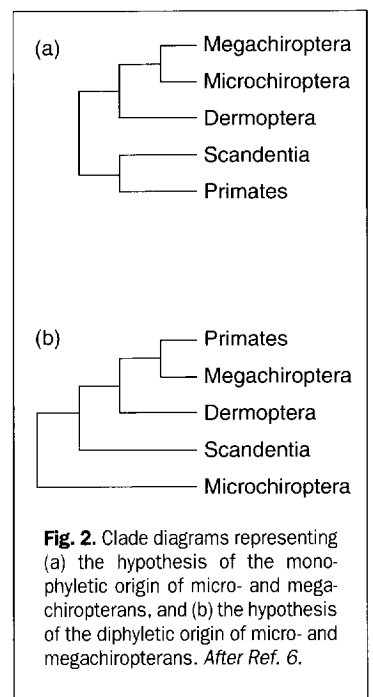


Fig. 2. Clade diagrams representing (a) the hypothesis of the monophyletic origin of micro- and megachiropterans, and (b) the hypothesis of the diphyetic origin of micro- and megachiropterans. After Ref. 6.

Box 1. Problems in the interpretation of motor pattern conservatism

Several problems with electromyographic studies have contributed to premature assumption of motor pattern stereotypy and homology.

First, the objective of detecting similarities has led to experimental designs that tend to minimize environmental variation and give a false impression of stereotypy^{22,23}. For example, in feeding studies using immobile prey, one quickly obtains a stereotypic motor pattern that may be misinterpreted as absence of a capacity for a flexible response and learning^{23,24}.

Second, when elusive prey are offered, motor patterns tend to be very similar among unrelated species, as in other activities that require large muscle forces. This similarity is owing to the nearly simultaneous activity of all muscles involved, protagonists and antagonists alike²⁵⁻²⁷. The crushing of hard prey – the motor pattern of this behaviour was used as derived character in Lauder's²⁸ study of the evolution of motor patterns in centrarchid fishes – is another example of forceful activity requiring simultaneous excitation of all muscles concerned. Not surprisingly the motor pattern of crushing hard prey in centrarchids closely resembles that in cichlid fishes²⁵, despite a totally different crushing mechanism¹⁴. Thus, forceful activities easily lead to an overestimation of similarity and stereotypy, and consequently give a false impression of motor pattern conservation.

Third, frequently only a few muscles are measured that are easy to reach when implanting electrodes, and a careful selection of the appropriate muscles is lacking.

Fourth, experimental ontogenetic studies, necessary to establish that the heritable component of a behaviour is considerable, are usually lacking. One cannot overemphasize that to appreciate the importance of phenotypic plasticity and learning in patterning muscle activity, ontogenetic analyses should be carried by varying the conditions (and possibly by using invasive techniques²⁹). Analyses in which development is followed, while only one type of prey is provided, are not sufficient to conclude that feeding appears to be stereotyped, developmentally fixed, unlearned and, thus, innate³⁰.

Finally, one must evaluate motor patterns in a phylogenetic context before one can evaluate the homology of patterns^{20,31,32}.

that liberate ventral snout movements from dorsal snout movements provide a compromise between the mechanical demands of fossoriality and the demands imposed by a larger gape size and increased food transport. Cundall¹⁵, thus, supports Greene's¹⁷ hypothesis that early snakes exploited large, but elongated, prey, with few major changes in the structure and function of the feeding apparatus from that of their lizard ancestors. Cranial characteristics in *Cylindrophis* are preadaptations for the increased kinesis of more advanced snakes. Extreme cranial kinesis, which allows snakes to feed on very large prey items¹⁸, developed later in the evolution of more advanced snakes according to this scenario.

Homology of motor patterns

Not all contributions of functional morphologists to evolutionary studies are plausible. When judging the appropriateness of a characteristic for cladistic studies, ideally one would know the heritable component of a character and the extent of phenotypic plasticity. This has turned out to be a problem in many studies in which motor patterns (electrical activity patterns of contracting muscles) are used in the construction of evolutionary scenarios and cladograms. It is sometimes questionable whether similar motor patterns of related groups are homologous and, thus, can be used to infer evolutionary constancy or change of characters¹⁹⁻²¹ (see Box 1). Although some motor patterns are clearly stereotypic and heritable (e.g. displays that serve communicative functions^{21,22}), the importance of variability due to phenotypic plasticity has been underestimated in the past. Recent studies have exercised greater caution in the interpretation of motor patterns and demonstrate a heightened awareness of the importance of learning and flexibility (see Refs 22-25, 29,33,34).

Evolutionary processes

Structural innovations

Structural innovations are often supposed to play an important role in the development of evolutionary radiations by triggering a cascade of diverse structural changes. Naturally, changes in the environmental context, such as the invasion of new habitats and the emergence of novel prey, also play an important role. It is therefore fruitful to study structural novelties in a phylogenetic and ecological context.

Structural innovations are inferred from phylogenetic patterns. Such innovations can be small and therefore hard

to detect without consideration of the functional context, but nonetheless can still have an enormous effect. One such innovation that occurred independently in mammals and birds is an increase in the size of vertebral transverse processes and a shift of attachment of locomotory muscles from the ribs to these processes³⁵. This shift allows respiration during sustained vigorous locomotion. In lizards (and early tetrapods) there is a constraint on simultaneous running and breathing. Lizards breathe by actively moving their ribs to change the volume of the thoracic cavity. Their hypaxial muscles are attached to

the ribs and during breathing they contract simultaneously. When running, however, the left and right hypaxial muscles contract alternately (Fig. 3). This imposes a constraint on running and breathing at the same time, which was demonstrated experimentally by Carrier³⁵. In birds and in mammals, the decoupling of locomotion and respiration was accomplished by the shift of locomotory muscles away from

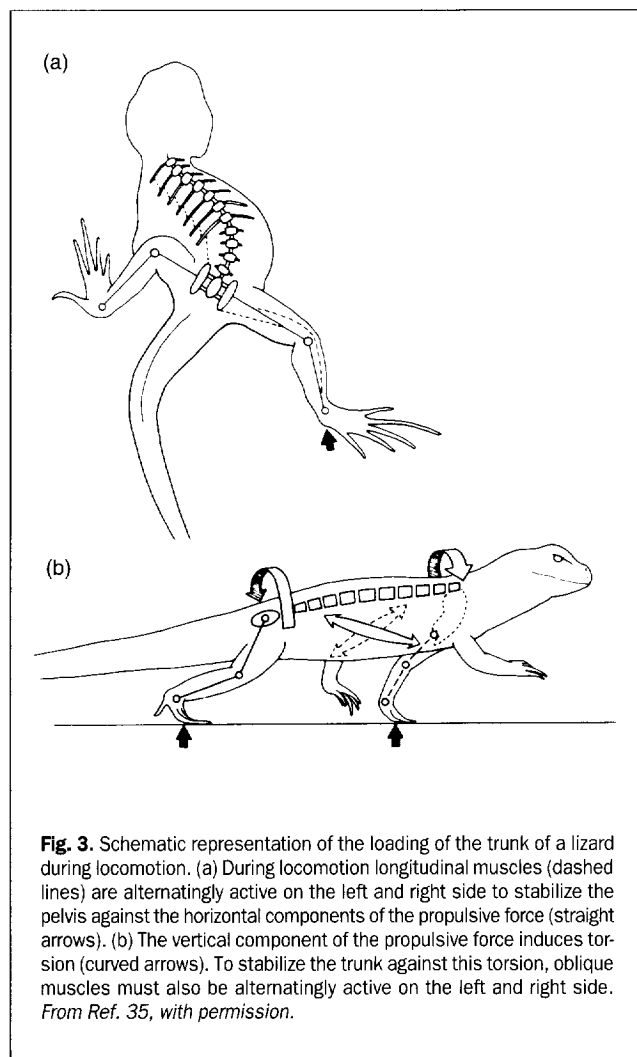
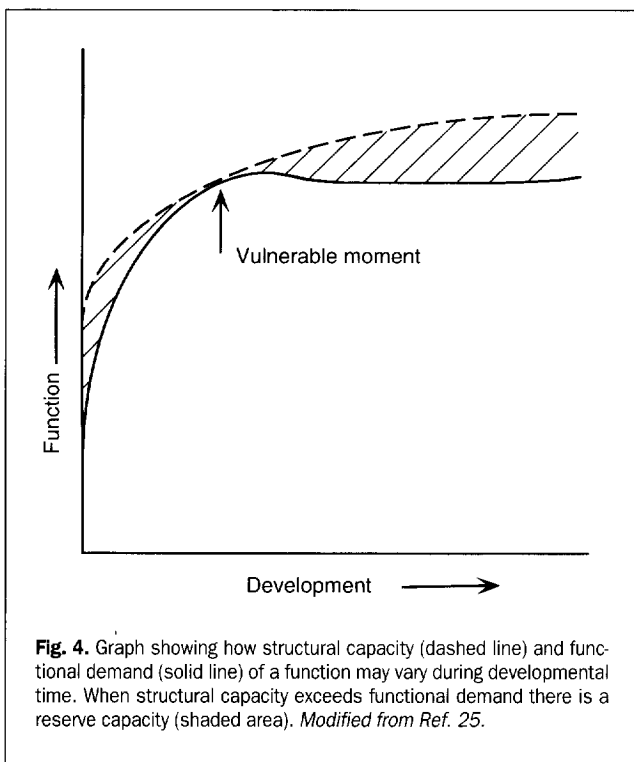


Fig. 3. Schematic representation of the loading of the trunk of a lizard during locomotion. (a) During locomotion longitudinal muscles (dashed lines) are alternately active on the left and right side to stabilize the pelvis against the horizontal components of the propulsive force (straight arrows). (b) The vertical component of the propulsive force induces torsion (curved arrows). To stabilize the trunk against this torsion, oblique muscles must also be alternately active on the left and right side. From Ref. 35, with permission.



the ribs to the vertebrae, emphasizing the evolutionary importance of this structural innovation and the relative ease of overcoming such a constraint.

As in the previous example, structural novelties are often structural decouplings^{36,37}. Such decouplings release mechanical constraints of structural and functional coupling. Vermeij³⁸ (see also Ref. 36) hypothesized that decouplings facilitate diversification and speciation by increasing the number of degrees of freedom and allowing more mechanical solutions for functional problems. Lauder³¹ emphasized the importance of testing this hypothesis in a phylogenetic context.

An example of striking morphological diversity and speciosity associated with a structural decoupling is provided by cichlid fishes (and other Labroidei)¹⁴. Liem³⁹ hypothesized that the versatility of the pharyngeal jaw apparatus is a key factor in the explosive radiation of cichlids into a seemingly endless number of feeding niches. Indeed, on the one hand, the versatile pharyngeal jaw apparatus allows cichlids to eat a wide range of prey types, enabling them to survive in adverse and changing environments; on the other hand, the bauplan is versatile in that only small evolutionary changes are necessary to make it suitable for the processing of novel prey items³⁹. Jensen⁴⁰ supports this scenario by showing that the unrelated exocoetoid fishes (Beloniformes), which possess a similar pharyngeal jaw apparatus, are more speciose than their sistergroup within the Beloniformes, the Scomberesocoida (>135 species versus 36). Liem³⁹ proposed the shift of insertion of one of the levator muscles as the key innovation in the development of the flexible pharyngeal jaw apparatus. Galis and Drucker¹⁴ modified the scenario of structural changes, suggesting that the decoupling of the upper and lower pharyngeal jaws is the initial structural innovation that enabled a cascade of successive changes. Regardless of whether the key evolutionary event was, in this case, structural or environmental, the decoupling seems to be the key structural innovation, because the coupled pharyngeal jaw apparatus of generalized perciforms is much more limited in its possibilities for movements than that of the derived cichlids, and its bauplan allows far fewer themes of (evolutionary) diversification.

A second type of structural innovation is the acquisition of a new structure – for example, the osseous fibular crest in theropod dinosaurs and birds⁴¹. This osseous crest is an ossified sesamoid cartilage rudiment. Sesamoids and secondary cartilages are formed when connective tissue is subjected to pressure and tension. Müller⁴¹ postulates that the pressure and tension on connective tissue of the limbs of theropods increased during evolution as a result of the progressive reduction of the fibula. The newly emerged sesamoid itself induces ossification at a later stage of development. Müller⁴¹ and Müller and Wagner⁴² discuss the generation of new structures from a developmental point of view and list examples of new structures.

A third type of structural innovation is the loss of a function by a structure that subsequently becomes available for a new function or for increased specialization of an already existing function. In a recent study of squamate reptiles⁴³, prey capture with the tongue (as in the extant iguanians) is shown to be primitive, whereas the derived mode is prey capture with the jaws (scleroglossans). The loss of lingual prehension is hypothesized to have enabled impressive chemosensory specialization of the tongue in scleroglossan reptiles^{32,43}.

A fourth type of structural innovation is the duplication of structures, followed by specialization of the repeated structures for different functions⁴². Examples are the differentiation of gill arches in fishes and the teeth in mammals⁴². Duplications of structures, like structural decouplings, increase the number of independent elements and potentially increase the diversifiability of body plans. One expects, therefore, that these types of structural novelties are most important in the evolution of radiations.

Mechanisms that allow the incorporation of evolutionary novelties

The incorporation of evolutionary novelties into the integrated organism will be constrained by many interacting form–function relationships. Organisms must have mechanisms to maintain the match between form and function during evolutionary changes. The most fruitful way to study this problem is to make use of the parallel between developmental and evolutionary changes. Mechanisms that maintain the match between form and function during development will at the same time facilitate evolutionary changes^{25,44}. The following mechanisms can be distinguished.

Excess structural capacity. The simplest mechanism facilitating the incorporation of evolutionary novelty is the use of excess structural capacity^{24,25}. There are several functional reasons why excess capacity might be expected at some time during the ontogeny of an organism.

- **Variable environments:** The structural capacity of organisms should be greater in variable environments than in more constant environments. In relatively constant environments, an organism can tolerate a low margin of safety because it has a small chance of having insufficient capacity during its lifetime^{45,46}.
- **Multiple functional demands for structures:** It is likely that satisfying several functional demands in one structure will constrain an optimal design for each separate function and may, therefore, result in an excess capacity for some functions.
- **Developmental mechanisms:** The size of the reserve capacity of individuals varies during ontogeny because functional demands are not constant and at times change quite rapidly^{24,25} (Fig. 4). Instantaneous changes in structures to meet varying demands are impossible and, therefore, at times excess structural capacity must be present to ensure

Box 2. Excess capacity during neuronal development

Nervous systems consist of populations of neurons that synapse precisely on other populations of neurons (e.g. Ref. 47). The developmental process in vertebrates that ensures a precise match is the creation of a large excess of neuronal cells followed by selective cell death, presumably of those neurons that lose the competition for a neurotrophic factor from target cells (e.g. Ref. 48). When a limb or sensory organ is lost, fewer neurons survive. Conversely, if the neuronal target area is larger, more neurons survive. This developmental process greatly increases the potential of organisms to evolve⁴⁷.

a sufficient capacity throughout life (Fig. 4). A striking example of a developmental mechanism leading to temporary excess capacity is found in the nervous system (Box 2).

Decoupling of developmental pathways. The potential of cells to develop into different types declines during development and their fate becomes increasingly irreversible. This irreversibility constrains form–function changes⁴⁹. One mechanism that can overcome this constraint is construction followed by cell death and new construction^{49,50}. This mechanism plays a particularly important role in animals with complex life cycles, that is, where the larvae have a totally different lifestyle to the adults. During metamorphosis, many larval structures degenerate by cell death and new adult organs develop^{49,50}. The result of this mechanism is that specializations for larval life are not compromised by functional demands of adult life and *vice versa*^{49,50} (Box 3).

Decoupled developmental pathways not only occur sequentially, as in metamorphosing animals, but also simultaneously. For several fish species, there is evidence that the growth and development of the sensory system is decoupled from somatic growth^{52,53}. This type of decoupling may facilitate evolutionary change by preserving the integrity of one complex in the face of changes in another.

Variable developmental pathways. Developmental pathways are often more variable than the characters they produce⁵⁴. Examples of variable developmental pathways are found in related organisms that are very similar as adults, but differ considerably as juveniles (see above). However, here I am concerned with the potential for variation within an individual. The evidence for plasticity of development within an individual comes mainly from regeneration experiments⁵⁴. Regeneration processes often differ from normal development and in addition they can be variable: for example, the sequence of appearance of structures during the regeneration of the pelvic fin in the blennioid fish *Salaria pavo* varies depending on the injury⁵⁴. Variability in developmental pathways suggests the importance of local organization in response to environmental conditions.

The potential for different developmental pathways provides a buffering mechanism against variations in the environment during ontogeny⁵⁴ and evolution.

Phenotypic plasticity. Phenotypic changes that depend on the environment (phenotypic plasticity) form a broad

Box 3. Decoupling of developmental pathways

Decoupling of developmental pathways allows a progressive evolutionary divergence of larval and adult characters because selection for larval and adult characters will not directly interfere with each other^{49,50}. An interesting example of the release from adult constraints is the polyploidy in the larvae of the higher Diptera⁵⁰. Since the adult is formed from different cells, their larvae can afford to be made of polyploid and polytene cells that cannot divide, but that have an increased metabolic rate and larger cell size. Another frequently suggested example of the evolutionary significance of developmental decoupling is the evolution of direct development (no larval stage) from an ancestral condition in which larvae were present^{49,51}.

category of variation. There is some overlap with the above-mentioned mechanisms, because buffering mechanisms do not always preserve the constancy of adult characters, but can also lead to changes and, thus, to phenotypic plasticity. Phenotypic plasticity facilitates evolutionary change both by providing a flexible response to environmental changes and by accommodating structural changes.

In particular, learning has a great influence on evolvability⁵⁵. This throws a different light on the controversy described above concerning the relative importance of conservativeness versus flexibility in muscle activity patterns. It seems likely that flexibility and learning in the development of such patterns play an important role in accommodating structural and behavioural changes that occur during development and evolution²⁵. More fine-scaled analysis of the development of muscle activity patterns may reveal modulation of patterns to a much larger extent than is now known.

The examples of developmental mechanisms that facilitate the incorporation of evolutionary novelties strongly suggest that development and evolution of complex organisms are possible thanks to a high degree of decoupling and autoregulation, in combination with an excess of building materials. Decoupling protects the integrity of decoupled units against the effects of changes elsewhere. Autoregulation facilitates decoupling and promotes coordination both within units and within the rest of the body by responding locally to the environment.

Transformation morphology: a new approach in functional morphology

Some of the contributions of functional morphology discussed above are based on analyses in the classical functional morphological sense: that is, the organism is studied as it is now or must have been before it was fossilized. In a new approach of functional morphology, the nature of the changing relationship between form and function during ontogeny and evolution is examined. This is achieved not by merely providing an understanding of successive stages in functional morphological respect, but by understanding the transformation itself, by constructing biomechanically feasible transformation schemes, by studying key structural changes that break important constraints enabling a cascade of changes, and by studying the mechanisms that preserve the match between form and function during ontogenetic and evolutionary change. This new approach, which could be called transformation morphology, is an invaluable contribution to the field of development and evolution.

Acknowledgements

This work was supported by a grant of the Dobberke Foundation for Comparative Psychology. I thank Jacques van Alphen, Michael Bell, Paul Brakefield, Carel ten Cate, Ian Hardy, Allen Herre, Hans Metz, Kurt Schwenk, Ole Seehausen, Jan Sevenster, Andy Sih and Günter Wagner for helpful comments on the manuscript and David Cundall for information on the evolution of snakes.

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