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The form-function relationship of vertebrates : A selected review

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Abstract. A selected literature dealing with the relationship between vertebrate structures and functions has been reviewed. Published literature in this field generally relates to three approaches: evolutionary, ontogenetic and holistic. This paper explains the salient features of these approaches and how their findings can be verified experimentally. Evolutionary approach can only make use of theoretical explanation, whereas, in both ontogenetic and holistic approaches experimentation is possible.

Keywords. Vertebrates; form-function relationship; evolutionary approach; ontogenetic approach ; holistic approach.

1. Introduction

The study of the relationship between vertebrate structures and functions, also referred to as "form-function relationship analysis", is becoming more a part of morphological research than gross anatomy. Published literature in this field generally adheres to three approaches: evolutionary, ontogenetic and holistic. The purpose of this paper is to review selected literature, that explains the important aspects of those approaches and how their findings can be verified experimentally.

1.1. *Evolutionary approach*

Evolutionary approach to the form-function relationship is not a new one. Böker (1935, 1936) establishes that form is derived from function; thus accordingly, function always precedes form. Consequently, he defines that the aim of research should be to describe the functional series, and that along with the phylogenetic development of function concurrent development of form occurs. But, Böker's views are not comprehensive because he considers only the functional aspects of form while neglecting the influence of genetics and convergence. Most of the functional anatomists started as evolutionists (Eaton 1935; Hofer 1948; Gans 1952, 1960; Bock 1959, 1964; Davis 1949, 1958, 1964; Gutmann 1966, 1967, 1968). Their research is mainly based on the shape or structure of living organisms. They consider the function or change in the function as parameter of the structure, therefore, any change in the structure causes parallel development in the function or evolution.

Bock and DeWitt (1959), in a study on the position of the toes in birds in relation to their locomotion, distinguished six types of toes which perform two functions, climbing and perching. Those six types of toes are all irregularly distributed over the taxonomic groups. Bock and DeWitt are of the opinion that the various types of toes have developed under the influence of selective forces of function (functional requirement). Bock (1960) considers the supplementary joint between the lower jaw and the cranium to be a pre-adapted structure which is a bracing mechanism that withstands the strong force exerted on the lower jaw during prey-catching. Gans (1952, 1960, 1966) has given similar evolutionary approach to functional anatomy. According to him a general body plan is formed genetically, upon which the functional influences are logically superimposed to develop the modified structures. Another evolutionary approach considered by Liem (1967a, b, 1970) combines comparative and deductive methods. Greenwood (1965) has correlated the environmental effects on the pharyngeal gills of cichlid fish. His work researches the adaptive strategies in the pharyngeal jaws based on the effects of the natural environment. Additionally, mosaic evolutionary approach has been postulated by DeBeer (1954) in which he indicates that the transitional changes do not involve a single organ-system but are rather functionally integrated structural complexes. For example, modifications in the feeding mechanism generally include changes in the skull, jaw musculature, and circulation. In describing the evolution of bony fish, several authors have emphasized the specializations and adaptations of the skull (jaws) and the muscles. The bony fish tend to optimize these structures of the head for food intake (Schaeffer and Rosen 1961).

1.2. *Ontogenetic approach*

Several functional morphologists have interrelated the developing elements at specific ontogenetical stages. Even in their developing stages, the elements are integrated in a pattern by their properties. These properties have been subdivided into coherence, presence, position, size and shape (Dullemeijer 1974).

It has been suggested that the individual parts of living organisms must develop in coherence with each other. To illustrate this, Milaire (1963) and Landsmeer (1968) have established a coherent system of phalangi with their surrounding tendons and muscles in a developing hand. Accordingly, the parts are arranged in specific positions in a limited space. The specific position and spatial coherence are needed for the parts to realize their function.

The simultaneous occurrence of several elements or organs seems to fulfil the functional demand of a growing organism. The functional interdependence of two specific elements like muscles and jaws in the amphibian larvae has been confirmed by Gaupp (1905), Sedrå (1950) and DeJongh (1968).

Elements develop as a result of the differentiation of homogeneous materials into heterogeneous structures. Heterogeneity of structures evolves at different stages of development. Wolpert (1968) has suggested the process by which a heterogeneous area evolves from a homogeneous one.

Elements may be divided into dominant and subordinate sub-groups. The dominant elements have a strong influence in early development. In the head the central nervous system seems to be dominant in all stages and is followed by the sense organs and the pharyngeal cavity (Dullemeijer 1971). Based on the dominance of surrounding mesenchymal tissue in the formation of mouth and the middle ear cavities, Goedbloed (1964) suggested that the formation of those cavities is controlled by the shifting of the epithelial border in relation to the mesenchyme. Thus, mesenchyme seems to be the dominant structure in the development of mouth and middle ear cavities. However, an opposite viewpoint has been put forth by Moss (1971), who suggests that oral and middle ear cavities influence the formation of mesenchyme. Moreover, the importance of the presence of the surrounding elements has been observed by Blechschmidt (1955) in the descent of a male gonad. Thus, a certain morphological arrangement is essential for a male gonad to descend.

The position of the elements in the process of ontogeny is also significant to their functions. Werner (1958, 1959) states that the position of the elements shifts greatly during ontogeny in order to carry out their activities. The specific position for the specific element is essential to carry out certain functions in a particular spatial arrangement (Landsmeer 1968). Therefore, position of the growing elements is related to their functions. As some elements are dominant they influence the position, form and structure of other elements. Such influences have been indicated by DeJongh (1968) and Moss and Salentijn (1969a, b). Moss (1968c) suggests that the positions of many growing skeletal elements are passively displaced because of the growth of other elements. Positional changes of the elements influence the determination of the general body plan (Moss and Young 1960; Moss and Salentijn 1969b).

Size also influences the process of development. Balinsky (1965) establishes a correlation between the amount of yolk and the process of gastrulation. The size or the amount of yolk determines the process of cleavage and gastrulation. The change in the size of an element such as a muscle will have a functional effect (exertion) on the other element (e.g., on a bone). Moreover, the change in the size will have impact on the shape of the local elements (Dullemeijer 1974).

The shape of the skull changes under the influence of muscle attachments and the weight it carries. The skull of pigs and elephants may be cited as examples (Dullemeijer 1974). The shape of a developing jaw is influenced by the size of the muscle attached to it. Moss and Salentijn (1969b) indicate that the general shape and position of an element depends on the position and size of other elements (e.g., the position of the jaws depends on the oral cavity and the position of the calvaria bones depends on the size and shape of the growing brain).

A switchover in the properties of an element has been observed by Claes (1964, 1965). He suggests that the chorda carries out the inductive function at an early stage but the same structure transforms into a supporting bar at a later stage. Such structural and functional switchovers in the elements are not infrequent. For example, during the endochondral ossification the cartilaginous structure is transformed into a bone.

Thus, during the process of ontogeny one can observe a spatially coherent system and interdependence of the developing elements with respect to their position, size and shape. The most important requirement of the elements is to carry out their functional demands.

1.3. *Holistic approach*

Recently, the functional anatomists have applied a holistic principle to the functional analysis of form. The holistic principle in its most modern form has been initiated by Van der Klaauw (1945, 1948, 1951, 1952). He was the first to introduce the concept of holism in modern morphology and was followed by Moss (1958, 1959, 1960, 1961b, 1968a, b), Dullemeijer (1956, 1958, 1959, 1974), Goss (1964), Dutta (1968, 1975, 1979a, b, 1980), and Osse (1969). There is, however, a difference of opinion amongst the functional morphologists regarding holism in relation to form and function. For example, Russell (1936), Smit (1961) and Goss (1964) believe that the specific structures develop after the influence of the function, while Bock (1959) postulates that function is caused by structures. On the other hand, Rensch (1948, 1958, 1960, 1972) formulates that there may have been structures without a function and, in turn, the non-functional structures may acquire new functions. He believes that a causal relationship exists between function and form though most other modern functional anatomists reject such a relationship (Barge 1919, 1936).

In order to correlate form and function, the head has been considered to be composed of several functional components which form a totality (Dutta 1975). The "functional component" has been described by Van der Klaauw (1948, 1951, 1952) and Dullemeijer (1956, 1958, 1959, 1971) as a morphological structure of an element which performs a certain function. According to Klaauw (1945), Dullemeijer (1956) and Dutta (1968, 1975) the components have a well-defined individuality which is determined by the components themselves and by the pattern of the skull. The components of the head are in turn composed of closely related elements such as bony elements, ligaments, muscles and other tissues which perform one or more functions together as mentioned by Bock (1964), Liem (1967a, b) and Dutta (1968, 1975, 1979, 1980). These functional units (elements) are connected and form couplings (Liem 1967a, b; Dutta 1975) which conduct the function of the animals.

Dutta (1975) has illustrated two such couplings in *Anabas testudineus* and *Ctenopoma acutirostre*. They are: (a) the levator operculi-opercular apparatus-mandibular coupling (regarded to cause depression of the lower jaw during fish respiration) and (b) the sternohyoideus-hyoid apparatus-interopercular-mandibular coupling (which collaborates with the former coupling during feeding).

A functional component cannot maintain its separate entity because in order to carry out its functions, it becomes involved with the elements of its neighbouring component(s) (Dutta 1975). This was further illustrated by Moss and Young (1960) who have conceived that the maxilla, which forms the orbit, is somehow related to vision while it also relates to the function of biting along the palatine. The interdependence of functional units is also emphasized by Gans (1969) when he states that, "The structures tend to be affected by the influence of multiple functions and any function will almost certainly affect multiple characteristics of an animal." This overlap between two or more functional components is not only limited to function, but also to structure as well as space.

2. Experimental analysis

Based on the philosophy of form-function relationship, several scholars have studied anatomy since the turn of the century. As early as 1903, Allis worked on the functional aspects of the skull, cranial, first spinal muscles, and nerves in *Scomber scomber*. Takahasi (1925), Tchernavin (1953), Holmquist (1910) and Edgeworth (1935) have also investigated functional aspects of structures. Their interpretations and conclusions were based on anatomy and visual observations. A new approach to the form-function relationship was established by Klaauw (1945, 1963) and followed by Dullemeijer (1974), Gans (1969), Liem (1967a, b), Barel *et al* (1976), Young (1969), Osse (1969), Sarkar (1960), Dutta (1968, 1973, 1974, 1975, 1977, 1978, 1979a, b, 1980). Elshoud-Oldenhave and Osse (1976), Lauder (1979, 1980a,b), and Lauder and Liem (1980). This philosophy in turn has become more apt to empirical experimentation with the introduction of electromyographic techniques and high-speed cinematography.

Within the last one and a half decades functional anatomists have begun to analyse experimentally the feeding and respiratory mechanisms of vertebrates. These experimental studies involve high-speed cinematography (Dutta 1968, 1975, 1979, 1980; Liem 1967b, 1970; Lauder 1979; Nyberg 1971).

It is well known that in many families of the bony fish, food is obtained by sucking (Alexander 1970). These movements are very fast (20–50 m second) and negative pressures from 100 to 400 cm of water have been registered (Hughes 1970). Therefore, a high speed, movie camera of 500–1000 frames/second is essential to make a precise recording of movements of the bony elements as well as the entire mechanism of prey intake of fish and other vertebrates. Food intake is the dominating function in fish populations and depends on the rapidness of movements of bory elements as well as the activity of their related muscles.

Synchronized electromyographic (EMG) and cinematographic techniques have been adopted by Ballintijn *et al* (1972), ElshoudOldenhave and Osse (1976), Lauder and Liem (1980a, b), Liem (1973, 1978), Liem and Osse (1975) and Osse (1969). Some authors have also used the cinematographic-electromyographic technique in higher forms of vertebrates (Kallen and Gans 1972; Weijs and Dantuma 1975). The usual cinematographic technique has been improved through the use of x-ray movies (Anker *et al* 1967). The x-ray cinematography is being extensively used by the researchers in Anglo-America as well as in Europe for the analysis of bone movements.

3. Conclusions

To establish form-function relationship all three approaches (evolutionary, ontogenetic and holistic) may be considered scientific, but there are relative advantages and disadvantages in their experimentation. Since verification of evolutionary findings is experimentally impossible, this approach deals with theoretical explanation. As different stages of development of an organism (including very minute, embryonic structures) are involved in ontogenetic studies, microscopic analysis, in addition to the application of electromyographic and cinematographic techniques, is necessary wherever required. Nonetheless, electromyographic technique is almost impossile to apply in small size specimens at the early stages of vertebrate development. However, since the holistic approach normally involves mature organisms it is generally possible to apply all three techniques (microscopic, electromyographic and cinematographic) without much difficulty.

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