J. Biosci., Vol. 19, Number 4, October 1994, pp 403-413. © Printed in India.

Concepts and methods in ecomorphology

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Abstract. An analysis of the concepts of ecomorphology is presented within a framework of areas of research in morphology, namely descriptive, functional, ecological and evolutionary morphology. A clear distinction must be made between functional and ecological morphology. The former is based on the concept of function and the latter on the concept of biological role. Although ecomorphology lies within the general area of evolutionary biology, explanations in ecomorphology are nomological-deductive and are distinctly different from explanations in evolutionary morphology which are historical-narrative.

Keywords. Morphology; functional morphology; ecomorphology; explanations; evolution.

1. Introduction

Avian morphology, together with the rest of vertebrate morphology, was a major focus of interest within avian biology during the last century and the first decades of this century. Work was directed toward a description and comparision of morphological form, with the results being used mainly for an understanding of avian classification. Although some authors, such as Fürbringer (1888), presented an elaborate phylogenetic tree for birds, very little attention was given to the phylogenetic and evolutionary history of birds by the comparative avian morphologists. During the 1930's interest in avian morphology, as with vertebrate morphology in general, decreased rapidly until by 1940 ornithologists actively engaged in anatomical research were becoming difficult to find. For example, although much of the early work in evolution after 1859 was carried out by morphologists, no real contribution was made to the evolutionary synthesis (1937-1948) by morphologists (see Mayr and Provine 1980). The reason for the decline in morphological studies was only in part the result of the growth of many new areas of biological studies made possible by the development of new techniques. Perhaps the major reason for the decrease of interest in morphology was simply because morphologists themselves never really understood fully Darwin's message and the basic concepts of evolutionary theory. Rather, they held on to the belief that it was possible to understand the evolution and classification of organisms through the comparison of purely morphological form. Therefore, morphologists were, in general, not interested in the analysis of function and in examining the details of the interrelationships between the diversity of organismic attributes and the demands of the external environment prior to the 1950's. I do not claim that no morphologists were interested in these areas of research before the 1950's; a few were, but they did not influence the theoretical or empirical development of the field. It should be noted that human anatomy had a tradition of a strong integration of form and function, which was essential for the practical application of human anatomy to medicine, but this approach was largely isolated from vertebrate morphology and especially from comparative and evolutionary aspects of this field.

Beginning in the 1950's, a slow change in approaches within vertebrate morphology started (see Bock 1990, for a historical review of these changes). One was the development of a functional anatomy using a diversity of observational and experimental techniques and asking questions that were more carefully framed (see Dullemeijer 1974). Important observational techniques included high-speed cinematography, X-ray cinematography, and electromyography (EMG). The first two methods permitted observation of movements of parts of the animal and the third method allowed the recording of the sequence and synchronization of muscle activities. Use of tread-mills and air-tunnels were important in studies of the functional morphology of vertebrate locomotion. The most important centers for the study of vertebrate functional morophology (including for birds) have been and still are the low countries (The Netherlands and Belgium), the United Kingdom, and North America (Canada and the United States). Research has concentrated largely on the skeletomuscular system of the locomotory and feeding apparatus. The growth of a broad-based functional vertebrate morphology was essential to other developments in morphology because a detailed knowledge of functional anatomy is critical to any real development of evolutionary morophology, including ecomorphology.

The second change in morphology beginning in the 1950's was the development of an evolutionary morphology. This development was undertaken largely by workers outside of the field of morphology, that is, by workers who had their primary training in fields other than morphology, namely systematics, evolutionary biology, or ecology. These workers were primarily interested in evolutionary or ecological questions and looked on morphology as a source of empirical data. To be sure, earlier workers has also approached morphology from positions outside the field (*e.g.*, Hesse and Doflein 1910-14; Nobel 1930; Stresemann 1927-34; Böker 1935-37; and a series of papers on birds based on Ph.D.theses done at the University of Berlin under Stresemann and at the University of California, Berkeley under Grinnell and Alden Miller), but these workers were not successful in changing morphology either because they accepted invalid evolutionary ideas, did not have the needed foundations in morphology (especially the required information from functional morphology), or simply did not persist in their research programme. Most of the students doing Ph.D. theses on evolutionary avian morphology in Berlin or in Berkeley did not continue a vigorous research program in this field.

More importantly, theoretical analyses of questions relating to evolutionary morphology were being published beginning in the 1950's. These included papers on mosaic evolution (de Beer 1954), preadaptation (Bock 1959), adaptation (Bock and von Wahlert 1965; Bock 1980), multiple pathways of evolution and paradaptation (Bock 1959, 1967) and major evolutionary change (Bock 1979). These and other papers provided a foundation on which to build concepts and approaches of evolutionary morphology.

During the 1950's and 1960's ecologists, working largely with birds, were analysing a series of related questions on the concept of the niche, habitat partition, community structure, diversity within taxa etc., and using simple morphological measures as tools with which to approach these ecological questions. These studies lead to the coining of the term "ecomorphology" in 1975 by Karr and James in a paper that examined the relationship of morphological features and environmental aspects strictly from the ecological side. The next year at a symposium entitled "Oekophysiologische Probleme in der Ornithologie", papers were presented by Bock (1977) and by Leisler (1977), which provided the essential links between the hitherto independent, but parallel developments in vertebrate morphology and ecology, and formulated some basic foundations and methods for a unified ecomorphology. Subsequent reviews of ecomorphology have been published by James (1982), Lederer (1984), Leisler and Winkler (1985, 1991), Winkler and Leisler (1985), Winkler (1988) and Bock (1990). A symposium on avian ecomorphology was presented at the 1986 International Ornithological Congress in Ottawa (see Bock and Winkler 1988).

2. Types of morphological explanations

2.1 *Introduction*

With increasing interest in morphological studies over the past four decades, a diversity of approaches have been developed under a variety of headings. It is important to identify and define these approaches and types of explanations in morphology to avoid chaos in forms of arguments, types of testing against empirical observations, and extrapolation of results and conclusions; this has not always been done and a considerable amount of unnecessary disagreement and confusion in morphological ideas have resulted (Dullemeijer 1980; Wake 1982; Alexander 1988; Bock 1988; Homberger 1988).

2.2 *Types of explanations*

Primary for any understanding of explanations in morphology or any other aspect of biology is a distinction between nomological-detective explanations (N–D E) and historical narrative explanations (H–N E; see Bock 1988, 1991a,b). This dichotomy is not quite the same as functional versus evolutionary biology, or proximal versus ultimate causes, as discussed by Mayr (1982:67-76) and by Dullemeijer (1980, 1985). Nomological explanations have the form that given a set of facts (initial and boundary conditions) and a set of laws, then a particular conclusion must follow. They answer the question of why or how a particular phenomenon has occurred. Or, put, in the opposite form, a particular phenomenon can be explained with a set of causes and a set of initial and boundary conditions. Nomological explanations apply to universals, do not depend on the past history of the objects or the phenomena being explained and their premises are assumed to be always true. Nomological explanations are tested in a deductive method in which predictions based on the set of facts and laws are tested against empirical observations. These explanations are maintained until they are falsified at which time substitute nomological explanations must be sought. Nomological explanations are the typical type of explanations used in chemistry, physics, most aspects of functional biology, and also in certain areas of evolutionary biology.

Historical explanations provide an understanding of the existing attributes of a particular object or set of objects at a definite point in time. They deal with the results of a set of processes, depend on the past history of these objects, and must be based on the pertinent nomological explanations. Objects explained by historical explanations are particulars (unique) in that they are composed of a finite set of objects having definite spatial-temporal positions. Historical explanations are generally stated in a non-deductive way in the hope of reaching the most reasonable explanation for the objects under scrutiny. Historical explanations are also tested against empirical observations partly in a deductive fashion by using intermediate nomological explanations, but much of this testing is inductive in nature with ever increasing evidence being collected in support of a particular historical explanation. Historical explanations include the evolution (or phylogeny) of groups of organisms or of particular features, biological classification, historical biogeography, etc.

2.3 *Descriptive morphology*

This aspect of morphological study includes the description of morphological form — the material composition and the arrangement of this material at all levels of organization (see Bock and von Wahlert 1965:272-3). Descriptive morphology may be the most difficult part of any anatomical investigation because it must be thorough and accurate, but must also cover those attributes necessary for understanding the functional properties, etc., of the morphological features. Unfortunately, description cannot be done simply for the sake of description, as the worker may not include the pertinent aspects. Hence much of the earlier descriptive avian morphology may not be suitable for current research projects. Unfortunately, too many current vertebrate, including avian, morphologists consider descriptive morphology of no importance and either do not provide descriptions or insufficient descriptions, a point made strongly by Homberger (1986, 1988).

Equally important is to understand the proper limits of the system of attributes of an individual organism, which comprises the coherent functioning unit (see Kraemer and Bock 1989; Bock 1989 a, b, c). Functionally interconnected complexes of attributes of the organism must always be studied together to assure that a reasonably complete understanding of the individual attributes can be achieved. Methods of connectivity explanations are difficult to learn, but they are essential as shown by the examples in Bock (1989a,b,c). A simple case is why in some woodpeckers with long tongues, the elongated hyoid horns pass into the right nostrill and extend to the front of the cavity inside the upper jaw, but in a few species (*e.g., Picoides villosus*), the elongated hyoid horns encircle the right eye. The explanation depends on the degree of specialization of the woodpecker species for drilling and, hence, or how flattened the bill is. In specialized drilling woodpecker, insufficient space exists within the cavity of the upper jaw for the hyoid horns and hence the elongated hyoid horns must assume a different course, such as to encircle the right eye.

2.4 *Functional morphology*

This second aspect of morphological analysis covers the description of morphological function—all physical and chemical properties of features arising from their form at all levels of organization (see Bock and von Wahlert 1965: 273-76, for a definition of the concept of function and its delimitation from that of biological role). The problem with any delimination of functional morphology begins immediately with the variation, disagreement, and ambiguity associated with the concept of function in theoretical biology, including evolutionary studies. Clarification of usage of the term function was a central part of the analysis of biological adaptation done by Bock and von Wahlert (1965). Yet, morphologists and evolutionary biologists continue to be most ambiguous in their use of the term function such as Pranger (1990) who writes with pride about a "pluralistic concept of function"—a position which I reject absolutely. Try to imagine development in physics with a pluralistic concept of force.

I take the firm position that terms used in biology must have clear and precise definitions and must stand for a single concept only. And I maintain that the definition proposed by Bock and von Wahlert (1965) for the term function captures the best central use of this term by most biologists.

Studies of morphological function can be and are usually best done in the laboratory under controlled conditions. Functional morphology has been the core in the rise of interest in morphology over the past four decades and quite rightly so. Workers in this area have made many important discoveries, and a real comparative functional morphology has developed. Functional morphology requires the use of many diverse techniques and sophisticated equipment and, although it is usually called "experimental functional morphology", most of the work is directly observational using sophisticated equipment and techniques.

A most important part of functional morphology, but one which has been downgraded by most recent workers is the correlation between properties of form and function of features (see Bock and Homberger 1988; Bock 1988; Bomberger 1988). Little work has been done on the form-function correlation because of the considerable lack of interest in descriptive morphology by most recent morphologists, This has resulted in a functional morphology of structural black boxes. This exists even in functional studies with extensive morphological descriptions as the necessary properties of form are not described or no attempt is made to correlate the observed properties of form and of function. By correlations, I mean attributes such as the relationship between particular properties of skeletal muscles and the force generation, or distance of shortening, or speed of shortening (Bock 1991b). These relationships must have a nomological form to be of any value to the morphologist. Once established, these correlations can be used to deduce functional properties of features in organisms for which the morphological form is known. That is, if various structural properties of skeletal muscles are known, then one can deduce functional properties such as maximum force, maximum distance of shortening, speed of shortening, etc. Knowledge of such correlations and the ability to deduce functional properties from known properties of form is essential if one hopes to reach functional and adaptational conclusions for morphological features in fossil species or in recent species that are not available for direct functional observations.

Note that functional morphology, including the establishment of form-function correlations are strictly nomological explanations. Moreover, these studies can be done on organisms under laboratory conditions; it is not necessary to have the organisms live freely in their normal environment. And studies of functional morphology are a necessary, but insufficient foundation on which to reach any adaptational conclusions.

2.5 *Ecomorphology*

Because of the newness of the field, a concise description of ecomorphology may not be possible. One definition is (Bock 1990: 262): "Ecomorphology is primarily concerned with analyses of the adaptiveness of morphological features and all dependent, correlated topics such as the comparisons of adaptations in different orgnisms, modifications of adaptive features due to competition and other causes, structure of ecological communities, diversity within taxa, etc". Another offered by Winkler (1988: 2246) is: "Ecomorphology deals with the covariation of morphology and ecology." This definition stems from the primary analytic approaches used by

Winkler and his associates, which are diverse correlation techniques used to investigate the observed variation in organisms and in environmental factors. Although simply stated, I feel that this definition is too broad because ecomorphology covers only a part of the interactions between environmental factors and organisms, and hence feel that restrictions must be placed on the boundaries of ecomorphology. For example, important interactions between organism and environment result in phenotypic changes in the organisms (= physiological adaptation, see Bock and von Wahlert 1965), This process is of real significance to evolutionary biology, but differs from the usual concept of ecomorphology (but see also, Witte *et al* 1990).

Ecomorphology differs from functional morphology in three major aspects, namely: (i) the basic concept is that of biological role (Bock and von Wahlert 1965: 278-9) rather than that of function; (ii) observations of organisms living in their natural environment are required, whereas functional morphology can be carried out completely on animals under captive conditions; and (iii) ecomorphology depends on the results of functional morphological studies, whereas functional morphology can be done independent of any information on ecomorphology. Many morphologists do not understand the necessity for a sharp distinction between functional morphology and ecomorphology (see, Wake 1982; Alexander 1988); this position is a direct consequence of their failure to comprehend the difference between the concepts of function and of biological role. Ecomorphology lies completely within the scope of nomological-deductive explanations.

An important component of ecomorphology which deserves special emphasis are behavioural studies that link traditional functional morphology with ecological investigations (see Moermond and Denslow 1983, 1985; Moermond and Howe 1989; Leisler *et al* 1987, 1989). These studies have shown that locomotory abilities are of prime importance in foraging, migratory and other activities of birds. Moermond and his co-workers have shown that the differing abilities of various passerine birds to reach food located at varying distances from a perch cannot be determined easily from the structure of the skeletomuscular system and, therefore must have important central nervous system control. These studies can be undertaken with a minimum of equipment and expense, yet the results are critical for the immediate development of ecomorphology.

Ecomorphology is not a monolithic field in its concepts, aims and investigative approaches because of the diversity of questions to be answered. At least two major approaches can be identified within ecomophology, but these are not necessarily exhaustive of all the possibilities. These will be discussed with suggestions on how to establish research programmes in each.

The first approach is basically the one of interest to workers from the morphological tradition (*e.g.,* Bock 1977). Its basic aim is the determination of the adaptiveness of complex morphological features and systems in individual species, followed by comparative analyses of these adaptations in different organisms, be they closely related or not. These studies are more traditional morphological and evolutionary ones. They begin with the morphology of the features under question. The first steps are usually a detailed morphological descriptions followed by a functional analysis. Then the biological roles of the feature and the environmental demands on the organism are determined by investigations carried out in the field on free-living animals. This portion of the study permits an estimation of the selective demands on the organism and therefore, a correlation between these selective demands and the properties of the feature as a means on which to base conclusions about the adaptation of the feature, including the degree of goodness of the adaptation (Bock 1980, 1993).

Because of the diversity of work that must be carried out in this research programme, successful projects generally require a team of workers with different specializations as discussed by Bock (1977). As a minimum, one member of the team concentrates on the descriptive and functional analyses and the other on the behavioural and ecological aspects. Most important is that the members of the team must interact throughout the study with feedback discussions between the different members of the team. This approach is well demonstrated in the analysis of the sublingual pouch in the nutcrackers *Nucifraga* (Bock *et al* 1973). Another example is the analyses of the lamellae in the bill of waterfowl with respect to filter-feeding. This work involved different groups not working as a team and not integrating their results. The functional morphology was done by Zweers and his co-workers (Zweers 1974; Zweers *et al* 1977; Kooloos *et al* 1989: Kooloos and Zweers 1991) and the ecomorphology by two different groups in Canada and in Australia (Crome 1985; Nudds and Bowlby 1984; Nudds and Kasminski 1984). The comparative investigations of lamellae spacing and prey size in different species of waterfowl were based on the initial functional studies by Zweers and used the assumption that details of the filtering mechanisms were the same in all species of ducks. However the later comparative functional studies of Kooloos *et al* (1989) and Kooloos and Zweers (1991) demonstrated that the details of filtering varied in different species of ducks which may well effect the ecomorphological conclusions. In a like fashion, the general assumption by ornithologists (*e.g.*, Jenkin 1957) that filtering was basically the same in waterfowl and flamingos is shown to be incorrect in a recent study by de Jong and Zweers (1981) and Zweers *et al* (1994), who showed that these two avian groups used quite different filtering mechanisms.

This approach does not represent the end point for ecomorphological analyses as commonly assumed by morphologists. Rather it provides the important information on details on functional properties and the adaptiveness of morphological features, which is essential for further ecomorphological investigations. I would like to emphasize that, aside from the simplest statements about the adaptiveness of features in birds, our knowledge about the adaptiveness of structural features in birds is sadly lacking. Hence, great care must be taken in ecomorphological studies to be discussed below.

The second approach is basically the one of interest to workers from the ecological tradition (*e.g.*, Leisler 1977; other cited papers by Leisler and by Winkler). Its basic aim is the determination of the pattern of adaptive features in taxa (best done in a group of closely related species such as members of a genus or a homogeneous family) as well as the determination of the composition of communities, niche structure, and other problems from the ecological side of ecomorphology. This approach deals with the covariation of morphology and ecology (Winkler 1988). In these investigations, the morphology used is generally far more simple that in the first approach and is usually confined to linear measures of external features (lengths and widths of bill, legs, wings, tail, etc.), simple area measures, such as wing surface, and linear measures (usually lengths) of bones. Simple, but generally valid assumptions are made about the adaptiveness of the feature or set of features being considered; these adaptive assumptions are generally broadly formulated. These assumptions, or better demonstrated conclusions about the adaptiveness of the morphological features, are the central important foundation for this approach to ecomorphology (Winkler 1988), and too frequently represent the weakpoint in the analysis (*e.g.*, Ricklefs and Travis

1980, in their concept of a morphological space). Leisler and Winkler (1991) provide a thorough review of this second approach to ecomorphology, including a full dicussion of the methods and a large bibliography of the avian ecomorphology literature.

The research program used in this approach (Winkler 1988) consists of the following steps: (i) Formulations of a hypothesis that predicts of correlation between a morphological trait(s) and an ecological condition(s). This includes statements on the presumed or demonstrated adaptive relationship and the proper selection of characters to be measured. (ii) Collection of relevant data from as many species and environmental conditions as possible and analysis of the data by suitable covariatation techniques in the attempt to falsify the predicted relationship as established under the first step. Measurements are taken on individuals from a series of usually closely related species, *i.e.*, members of a genus or of a family. In general few individuals per species need to be measured as the individual variation within a species is usually small compared to differences between species. Analysis is by some method of statistical correlation analysis such as principle components analysis. (iii) Explanation of the correlations found or why confirmation of the predicted relationship failed in the group of organisms.

This approach has been used highly sucessfully in a number of studies by Winkler, Leisler and their co-workers (see above citations), in which the overall similarity in features of diverse members of a taxonomic group and in their adaptive relationships to environmental factors was demonstrated. In addition, these workers have shown that this approach works best for comparisions of members of closely related groups such as genera and some families of birds. Comparisons of different groups with similar habits, such as the Old World Warblers (Sylviidae) and the New World Wood–Warblers (Parulidae), generally show that each group had adapted to enviornmental demands in different ways. This second approach is one that can be applied readily with a minimum of equipment and costs, but does require careful consideration of the groups examined, the hypotheses about the adaptiveness of features and complexes of features, and the sets of characters to be measured.

It must be stressed that ecomorphological analysis are nomological deductive explanations as the determination of the adaptiveness of features is a strictly nomological explanation. Comparison of these adaptations and other types of ecomorphological investigations are also nomological. However, the important aspect of all ecomorphological studies is that the organisms must be observed living normally in their natural environment and that correlations are made between attributes of the features of organisms and attributes of environmental factors acting on these organisms. Any study that excludes these observations of the organisms interacting with their environment could not be included under the overall cover of ecomorphology.

2.6 *Evolutionary morphology*

Evolutionary morphology covers a broad ‘range of morphological studies, including certain types of comparative investigations, systematics, and evolutionary history of features and groups. These studies differ from those discussed above in that they are historical-narrative explanations (Bock 1991a). It must be stressed that the frequent distinction between functional versus evolutionary biology is not synonymous with nomological versus historical explanations. Certain areas within evolutionary biology, such as part of all of ecomorphology, are strictly nomological explanations. Successful investigations in evolutionary morphology depend on good foundations of descriptive, functional and integrative morphology (for connectivity analyses, see Bock 1989b) and ecomorphology, and on well-established N—D causes and processes of evolutionary changes. Some methodologies and concepts of evolutionary morphology can be found in Bock (1979, 1981, 1989a, 1989c, 1990). Use of the concept of homology is a central, but not only, part in studies of evolutionary morphology.

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