FUNCTIONAL AND EVOLUTIONARY MORPHOLOGY

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Introduction

In 1956 anatomy was moribund; the field of functional and evolutionary morphology barely existed as a scientific discipline. The dawning of the era of molecular biology was apparent, and among anatomically inclined biologists there was a headlong rush into cell (especially ultrastructural) and molecular biology, or at least ancillary fields. Anatomical science can rightly claim to be the oldest area of biology, and any history of biology is filled with accounts of anatomically based discoveries and interpretations [1]. During the nineteenth century comparative anatomy came to reign supreme and included in its ranks the vast majority of biologists, working from the cell to the whole organismal levels of organization. But in the twentieth century the ranks of anatomists became progressively depleted. To a large extent this was simply the result of increased technical opportunity as well as the successes of the early anatomists in establishing a firm empirical base for more specialized investigations. It was inevitable that increased sophistication should also be accompanied by diversification. It was not that anatomical investigations were considered unimportant; on the contrary, so much was known that little challenge remained.

THE DECLINE OF ANATOMY

By the 1950s, anatomical science in the United States was centered largely in medical schools, although there remained a few strong laboratories in general zoology departments as well. The "gross anatomists" of medical schools were not in a very happy state, for although their

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service in teaching was essential, gross anatomical research was not held in high esteem. Unfortunate tendencies existed both in medical schools and in zoology departments to assume that any biologist who set his or her mind to it could teach gross human or comparative anatomy, and, since there were not many productive graduate programs in these areas, many individuals with research interests in relatively remote subjects were offered teaching posts. As a result, a self-fulfilling prophecy was promulgated and in many universities gross and comparative anatomy courses began to be taught as technical, rote-learning disciplines, with little intellectual content.

What I have described characterizes the United States perhaps more than other parts of the world, for such widely respected figures as Sir Solly Zuckerman and Wilfred Le Gros Clark in Great Britain proudly counted themselves as anatomists. However, the tendency to diminish the role and significance of anatomy was felt everywhere. Anatomists were made to feel "old-fashioned."

How had the field come to fall on such hard times? I think it was largely the result of a century-long trend toward reductionism. As we became more and more able to probe microstructure, ultrastructure, and finally even molecular structure, those with interests in the structural and functional foundations of biology simply moved to greener pastures.

Certainly it cannot be said that the field inherently lacked intellectual discipline and stimulation. Many have written accounts of the intense stimulation provided by anatomical studies. Others have written wistfully of the departure from the center stage of comparative anatomy. For example, Medawar and Medawar [2, pp. 19–20] write, "The modern impatience with research as slow moving as comparative anatomy must not be allowed to distract attention from the fact that the study of comparative anatomy is an exacting and formally very beautiful discipline. Indeed, in the hands of some of its greatest practitioners it became almost a biological art form: a biologist who cannot appreciate and marvel at Edwin Goodrich's *Studies in the Structure and Development of Vertebrates* (Dover Press, 1930) deserves sympathy." These authors attribute the decline of comparative anatomy simply to the apparent fact that "the greater part of the work has already been done."

In a sense, then, anatomy as a cohesive science slowly died. It remained a discipline taught to medical students, usually in three parts—gross anatomy, histology, and neuroanatomy. Many outstanding scientists continued to call themselves anatomists. But studies of structural biology became so diffuse that most of those who pursued them (as, for example, those who studied the crystalline structure of proteins) no longer considered themselves anatomists, and frequently had no formal training in anatomy.

If anatomy in general was suffering from malaise and decline, those anatomists with primarily evolutionary interests were faring no better. The mid-1950s saw the publication of the last great volumes of what has been called the *Evolutionary Synthesis.* A generally acknowledged fact (well displayed in [3]) is that morphologists played no central role in the synthesis, although there are varying interpretations of the degree to which they influenced the proceedings [4]. Evolutionary morphology did not exist as a well-defined science, but there were many comparative anatomists with an evolutionary orientation. An outstanding American example was D. D. Davis [5] whose remarkably prescient analysis was largely overlooked.

The status of anatomy in general remained highest in Great Britain. The great traditions of comparative anatomy stemming from E. C. Goodrich sustained high-quality research work in evolutionary aspects of morphology from the invertebrates (notably by S. M. Manton) through the vertebrates (the great vertebrate paleontologist D. M. S. Watson was long professor of zoology in University College, London), including the primates (Le Gros Clark, Zuckerman, Ashton, and others). Equally important was the tradition of research in functional morphology, largely centered at Cambridge, which included such outstanding figures as Gray, Lighthill, and Lissman. But even in Great Britain pressures built for change. Molecular biology enjoyed outstanding success in the great British universities and laboratories, and pervasive changes began to be seen there as well as elsewhere in the world. For example, Watson's old department was gradually restructured to be dominated by immunological research. Still, the anatomical approach was sustained during critical periods, and it was in Great Britain that some of the first signs of the development of an essentially new field, functional and evolutionary morphology, were seen.

A RENAISSANCE OF MORPHOLOGY

Today we see in retrospect a renaissance in morphology. What seemed to be fading from the scene 25 years ago is today in a state of high vigor and great diversity. While morphologists have long relied on the comparative method, and in fact the comparative method may be anatomy's outstanding contribution to science in general, the new morphology incorporates as well the experimental method. I define functional and evolutionary morphology as that field of science which examines the evolution of form by combining comparative and experimental methods of analysis. The key element is the problem orientation of the investigator. In other words, integration of morphological approaches into analysis of specific problems in evolutionary biology is the main criterion in identification of this field.

I make some restrictions for purposes of this analysis. While I know of outstanding work at the cellular and subcellular levels that qualifies for my definition, I shall consider only the tissue and higher levels of biological organization in this essay. Further, I shall limit myself to a consideration of animal morphology.

Morphology Today

Morphology is, of course, the study of form, and in its purest state it deals with the materials of tissues, organs, and organisms as well as with the forces that mold them. When one examines these processes only in reference to essentially engineering principles (as, for example, in biomechanical analysis) and without respect to the modification of form in successive generations of the organisms studied, the science is not evolutionary. Biomechanics need not be an evolutionary science, and in fact many of the outstanding practitioners in this field function without paying much attention to evolutionary processes. Biomechanics is the epitome of the reductionist approach applied to morphology; it has generated much data. But I shall consider biomechanics to be a subdiscipline of functional and evolutionary morphology, for it has played an important role in the renaissance of morphology. The nature of biological materials and the constraints imposed on biological systems by the physical and chemical properties of those materials and by the environment in essence define the limits of problems in biomechanics. Scientists have been concerned with these problems at least since the time of Galileo, but perhaps the first modern biologist (or was he the most classical of all?) who addressed these issues in a comprehensive way was D'Arcy Thompson [6]. In truth, his treatise was widely unread, and it did not have much impact either when published or for long thereafter. But during the past 25 years, biomechanics has emerged at last and workers of great power and sophistication have contributed to the area. We now have texts that were written with the avowed purpose of combining mechanical engineering and biology, and at least one of these [7] includes evolutionary approaches (although these are descriptive and interpretive rather than analytical). Some important general books in the field favor analysis of adaptations [8–10], which I take to mean the "fit" (more or less from an engineering point of view) of organisms to environments. The book by Gans [10] is particularly instructive of the way in which one leading functional and evolutionary morphologist developed his own highly personal, idiographic, and effective approach to the field. In essence, the focus is on particular adaptations—egg-eating in snakes, locomotion without limbs, air-breathing in frogs—and a variety of approaches is used to illustrate the ways in which biologists analyze evolutionary "improvements." The emphasis is on adaptive themes and tuning of adaptations that already exist in gross form, rather than on the appearance of the adaptation per se.

Workers in the field of biomechanics often stress mechanical engineering approaches to the near-exclusion of other problems. Frequently the ultimate questions asked do not relate to fundamental evolutionary issues, but to explaining how an adaptation has come to have its particular form. For example, Wainwright et al. [7] consider at length the nature of rigid skeletal materials and note that the skeleton of echinoderms has unusual, and very great, porosity and that in addition it alone among all the metazoa has a stony skeleton that is not made up of polycrystals. What does this mean? The answer, they believe, lies in the area of ceramic engineering. Perhaps the trabecular structure would prevent cracks from running far, they suggest. Again and again the problem is seen first as one in some area of engineering. A strong implication is that if we fully understand the fabricational basis of an "adaptation," and the way it functions in the environment, the goal has been achieved. Still, I consider biomechanics to be one of the most vigorous and productive areas of modern morphology, including such applied subjects as biomedical engineering. In the future I expect functional and evolutionary morphologists will incorporate more and more the findings of biomechanics into their work as baseline information, but I do not look for any new evolutionary insights, simply because of the orientation of the workers in the field. The most promising developments are the attempts to relate biomechanics directly to ecology [11–13].

Biomechanics is so closely allied to functional morphology that some workers treat the terms as essentially synonymous. There is, however, a distinctly separate field of functional morphology. To me the dominant figure in functional morphology in the past 25 years is Peter Dullemeijer, leader of the famous Leiden group of anatomists. Dullemeijer is a deeply philosophical scientist who is focused very strongly on an independent functional morphology as a biological discipline. He has been profoundly important for two reasons. First, his own research in functional morphology is highly significant, and much of it appeared just at the beginning of the period I have been assessing [14, 15]. Further, Leiden has been a training ground for some of the most significant workers in modern functional morphology (including, as a small sample, Barel, de Jongh, Liem, Osse, and Zweers). Second, building on the tradition of his predecessors [e.g., 16], Dullemeijer has constructed a new and modern, holistic approach to functional morphology [17]. He is uncompromising in his attempts to define a conceptual framework for functional morphology as a discrete science.

In a recent essay, Dullemeijer [18] has specifically addressed the relationship of functional morphology and evolutionary biology. Because he is so explicit in his view that functional morphology is an entirely separate field from evolutionary biology (*"Functional morphology and evolutionary biology so far have their own domain and their own principles of explanation"* [18, p. 210]), his paper is an almost necessary point of departure. I believe that it is fair to state that perhaps the principal goal of most modern functional morphologists, especially those active in North America, is a melding of functional morphology and evolutionary biology (see [19]). In fact, many North American scientists (such as I) whose interests span morphology, systematics, genetics, and perhaps ecology, development, and behavior in various combinations refer to themselves as "evolutionary biologists," a designation that is not favored in Europe.

Dullemeijer outlines the main concepts of animal functional morphology as follows [18, p. 161], here somewhat abbreviated and modified): (1) form, which includes any form feature at any level of organization of animals; (2) function, here primarily and preliminarily taken as activities at any level performed or shown by animals; (3) functional component, the connection of form and function; compromise and integration enter here; (4) pattern, which can be visualized as a network showing the relations between the functional components and the particular elements constituting those components. Pattern is the relation between function and form. Examples are Dullemeijer's diagram of pattern in the head of crotalid snakes [17, fig. 62] and Liem's diagram of pattern in the head of a cichlid fish [20, fig. 12].

These concepts are seen as relating to two main areas of evolutionary biology, and much of Dullemeijer's long essay [18] treats the connections. The first of these is effectively the phylogenetic component of evolution, and deals with problems in interpretation of the history of life. The second is the adaptive component of evolution, and deals with processes responsible for change. I shall deal with both of these areas below.

The 1960s and 1970s witnessed a great resurgence of interest in morphology, especially in the combination used in the title of this essay. In the United States there was a surprising reversal of the trends of the 1950s outlined earlier. Courses such as comparative anatomy which had been dropped from curricula were reinitiated, and new courses in functional morphology, biomechanics, evolutionary morphology, and the like came into existence. The Vertebrate Morphology Division of the American Society of Morphologists was about the only organizational base for the burgeoning field, and from its establishment in 1960 it has provided a central focus for a large number of meetings and symposia. By the end of the 1970s a rather remarkable situation prevailed. There were clusters of functional and evolutionary morphologists throughout the world, and in the United States many had moved into positions of leadership in biology in general. Departmental chairmen at Harvard University, the University of Michigan, the University of Chicago, and elsewhere were morphologists, as were the directors of the Museum of Comparative Zoology at Harvard and the Museum of Vertebrate Zoology at the University of California, Berkeley. Strong schools existed at several localities in the Netherlands, Germany, France, Great Britain, and elsewhere. What these groups had in common was a belief that morphology was significant and important for modern evolutionary biology (as Dullemeijer [18] succinctly states: "For a neo-Darwinian evolutionary theory, contributions from functional and ecological morphology are indispensable"). Signs of the vigor of the field abound, not only in the texts cited above but also in a variety of symposia, for example, "Evolutionary Development of Form and Symmetry" (*Systematic Zoology* [1973]), "Models and Mechanisms of Morphological Change in Evolution" (*American Zoologist* [1975]), and "Morphology and Analysis of Adaptation" and "Analysis of Form" (*American Zoologist* [1980]), to list but a few. In addition, in the spring of 1981 a Dahlem Conference focused on "Development and Evolution." Without doubt much has been accomplished, and there is good reason for the enthusiasm many workers display. However, a well-defined field of functional and evolutionary morphology is more a dream than a reality at this point in history. There are few agreed-upon principles and the central concepts are broad and somewhat vague. The data of morphologists and some of their interpretations are important, even "indispensable" for evolutionary biology, but I do not yet see integration of morphology into the central themes of evolutionary biology at the level of understanding the processes responsible for the evolutionary modification of form and function. In fact, that is the main challenge of the field for the next 25 years.

Conceptual Organization

From the greatly increased activity in functional and evolutionary morphology, one might expect some commonly agreed-upon questions or research strategies. In fact, I perceive no small set of questions or approaches. There are groups of workers, often widespread, which share approaches and frequently techniques, but there are few central themes. In the following paragraphs I shall briefly outline some of the approaches that I perceive.

I earlier discussed the biomechanical approach. My strong impression is that workers in this field accept that evolution has occurred and that observed morphologies represent evolved responses to problems posed by the environment. In other words, they have as a point of departure the assumption that natural selection has led to the organism or structure under study. The questions asked concern the mechanical operation of a complex structure, or the material basis for the structure. This field takes advantage of technical innovation. Of concern are the crystalline nature of biological materials, the properties of various macromolecules important in biological structure, and physical principles applied to the structures at all appropriate levels of organization. Environmental factors often are considered in biomechanical analyses. For example, the biomechanics of the holdfasts of marine organisms can only be understood by incorporating analysis of such factors in the physical environment as ocean wave dynamics.

A second conceptual approach is strongly adaptationist. Practitioners often have come out of traditional morphological backgrounds. A major trend during the past 25 years is the recruitment of large numbers of paleontologists into functional and evolutionary morphology, many of whom share the adaptationist approach. Only a subtle distinction separates adaptationist and biomechanical groups; adaptationists at least claim to be interested in the *processes* of adaptation. At the present time the adaptationist approach is under fire [21], primarily because there have been excesses in the interpretation of nearly all structural features of organisms as adaptations in their own right, out of the context of the whole organism. When this is done the very concept of adaptation becomes meaningless. However, this is not an accusation that is fairly made for functional morphology as a whole. Certainly one of the key figures in the revival of interest in functional and evolutionary morphology was D. Dwight Davis, whose major work [22] is strongly holistic.

A third group of workers uses as its conceptual basis the idea that there is an independent science of form, and that it bears directly on evolutionary questions. There are nearly as many subgroups as there are workers, and I shall only try to highlight some of the approaches. Certainly Dullemeijer, whose approach was outlined above, falls into this category. Yet, Dullemeijer cannot be considered to be the central figure, for a recent assessment of the field [23] fails even to cite him. I would include the German school of constructional morphology [24] as another major subgroup. Constructional morphology perceives form as having three major causes: traditional (mainly developmental and phylogenetic), functional, and fabricational. The focus, however, tends to be on the fabricational, perhaps because this is where workers often go astray. Constructional morphology examines details of structure in an attempt to find clues about the ways in which developmental processes proceeded. Once a fabricational basis for structure is determined, limits are set on what needs to be explained. Constructional morphology is practiced mainly by workers with strong paleontological orientations.

Theoretical morphology is another subgroup. This approach seeks to limit the questions of morphologists by determining expectations of evolutionary processes from variations on a theme. The problem to be solved is to detect the theme and to characterize it in a few parameters.

Modifications of these parameters alone result in changes of form. The paradigm study in this area is Raup [25]. Because theoretical morphology is as yet a relatively new field, and one requiring a high level of mathematical competence, it has not attracted many workers. However, stimulating work on early embryonic morphogenesis [26] is a good example of a recent application of this method that shows great promise.

A final major subgroup might be termed developmental evolutionary morphology. This area was given major impetus by the publication of Gould's *Ontogeny and Phylogeny* [27], but many workers were conducting studies in the area before that time. This group of workers assumes that gaps exist in adaptive "space," and that all conceivable forms do not and cannot exist [28]. They then proceed to attempt to understand the rules of development which give rise to particular form, and to both interpret past events and predict future trends from this perspective.

A completely separate conceptual approach to morphology is the use of morphological data as "characters" for the inferential reconstruction of phylogeny. One might argue that this is systematics, not morphology, and that I should not discuss it. But morphologists must confront the claims of this group, which essentially uses an epistemological argument in stating that severe limits exist on what morphologists can know, and how they can interpret their data. It is argued that discussions of evolutionary processes in the absence of soundly based hypotheses of cladistic (i.e., branching sequence in phylogeny) structure of the group under study are simply speculative or, worse, based on axiomatic acceptance of concepts such as natural selection and adaptation [29]. Of special significance is the fact that some of the major conceptual leaders were trained as morphologists and have come to see the field of functional and evolutionary morphology as relatively sterile. I have in mind particularly Gareth Nelson [30] and Joel Cracraft [29, 31], whose books are major contributions to systematics. Both properly stress that systematic hypotheses underlie every comparative study, and accordingly need explicit consideration in such studies.

This categorization is overly brief and doubtless there will be those who think that major areas have been ignored. Some believe that there is an evolving field of ecological morphology, which, for example, examines convergent adaptive arrays. Since most of the workers are either ecologists or morphometricians, there is typically very little morphology, and it is primarily descriptive and nonfunctional.

Prospects

Causes for the renaissance of interest in morphology are not hard to find. While the reductionist approaches of the middle part of our century have been enormously productive and progressive, there is a growing awareness of our need to study organisms more. While evolution occurs by means of changes in populations, it is the organism, after all, that evolves in an ultimate sense. It is the organism that lives in an environment. It is the organism that we most immediately perceive and want to understand. In the above paragraphs I have briefly outlined my perception of the foundations of modern functional and evolutionary morphology and the current foci of investigation. This essay is not meant to be a review or even a summary of the field, however. Rather, it is my personal assessment. Thus, in the remaining paragraphs I present my idiosyncratic evaluation.

Functional and evolutionary morphology is at a crossroad. On the one hand, there are morphologists who ask "how does it work?" and are content with proximate answers. They move from one finding to the next question, relentlessly adding to our empirical foundation. On the other hand are morphologists who ask "how has it come to work?" It is this group that worries about what to do next. Should one follow the deductive path advocated by, for example, Dullemeijer? Or should one start from particular cases to build up a generality?

My own career has involved following the second major pathway described above, and perhaps understandably I favor that approach. I am not dogmatic in this matter. For me the search for a science of form is still in its infancy, and despite the relative antiquity of the investigation we are far from an answer. I shall simply attempt to indicate what I consider to be crucial components for an independent science of form.

The reasons for the growth and development of functional and evolutionary morphology are not the product of elucidation of concepts or central questions. Rather, biologists have been drawn to the field because forms and functions are what work in the biological world. Forms and functions and their worlds must be at the center of biology, and for too long they were taken for granted, overlooked, or ignored. Now the challenge, as I see it, is to formulate central concepts and to build a science that does not simply serve evolutionary biology, but rather is central to it.

For too long morphology has been, as it were, a handmaiden of other disciplines. This is especially true of functional and evolutionary morphology. The field has prospered because others have found it useful. Physical anthropologists have felt that functional morphological data will be of significance in helping them analyze, for example, the evolution of upright posture. Yet, a single fossil footprint in conjunction with a small group of bones might be vastly more conclusive. Perhaps functional morphologists might help unravel the patterns of evolution of complexities of locomotory modes in primates, but cladists will argue that this cannot be done without cladistic hypotheses. However, the morphologists again can be useful, for they provide the data used to construct cladistic hypotheses. Paleontologists in general find functional and evolutionary morphologists useful in aiding them in their interpretation of the fossil record. Behaviorists find morphologists useful for they help define the limits of movements and the anatomical basis for complex behavioral acts. Ecologists find functional morphologists useful in helping them understand the morphological foundations of community structure. But there is more to an independent field of science than utility to some other field!

I applaud workers such as Dullemeijer for attempting to define a central framework for functional morphology [18]. However, when I analyze the progress that has been made in linking or integrating functional and evolutionary morphology I am left unsatisfied. Dullemeijer, a strong advocate of a deductive and holistic approach to functional morphology, is critical of attempts to integrate the field with evolutionary biology. For example, he considers in detail, and accurately, an approach that Lombard and Wake [32, 33] used to analyze the functional and evolutionary morphology of feeding mechanisms in salamanders. We were concerned with the evolution of highly protrusible tongues. We used a deductive method, first developing a model from theoretical considerations and observations and then using that model to make predictions for likely evolutionary pathways, given certain kinds of natural selection for increased performance of various kinds. From my perspective the study was fairly successful in a limited sense. Subsequent studies have clarified aspects of the perception of prey by these salamanders [34] and the physiological basis for observed movements [35]. The results conform well with previous hypotheses concerning evolutionary relationships [36, 37]. However, we did not measure performance in the field, and from available information concerning food habits of salamanders it is unlikely that degree of morphological "specialization" has a direct association with specialization of food. We do not know whether we should expect differences in what salamanders eat, in where they eat, in how they eat, or in all of these categories. But if we want to demonstrate that natural selection is the process that has produced the morphological specialization, we must at least attempt to show the advantage of one organism relative to another [29]. Further, we ought to be concerned with the nature of variation likely to occur in a local population, as well as the genetic and developmental basis for such variation.

Dullemeijer is critical of attempts to make interpretations such as some of those above because he argues that one becomes circular in going from deductive to inductive systems of reasoning [18]. Too many assumptions are made when we assert that natural selection is responsible for a particular pattern, and when we assume that only a particular kind of evolution has occurred. But a purely deductive approach, such as Dullemeijer advocates, seems too extreme to me. The optimization theories used by Dullemeijer have been effectively criticized by Liem [38], who argues that organisms in the real world make do with the best available, very likely suboptimal morphology (cf. [39]). Liem advocates a pluralistic approach that takes into account factors that limit optimization but enhance versatility of function, which he believes to provide the "matrix upon which natural selection can act."

I admire the purity and rigor of Dullemeijer's method, and I acknowledge that problems arise with pluralism. But it is evident to me that functional morphologists have a unique opportunity to integrate their studies into evolutionary biology. Perhaps the major problem for the future is that of the origin of adaptations, a much-studied but elusive topic. A key component of the study of adaptation is the recognition that not all possible morphologies occur, and many are impossible. I strongly believe that a variety of constraints set direction of evolutionary change for each system studied. Some of these have been discussed directly for our tongue example [32, 33, 40]. Constraints have been categorized as historical (essentially the results of unique historical "accidents"—events often unrelated to the form and function under study), developmental (it is well known that development is a system of complex feedback tending to produce a standard form despite perturbation), and architectural (or fabricational, having to do with the materials of form and their construction) [21]. A different approach by Hickman [41], focused on a particular problem (the reasons for different radular patterns in gastropods), usefully treats constraints [21]. She identifies seven factors contributing to form and pattern and well exemplifies a "pluralistic" (as opposed to "adaptationist") approach to functional and evolutionary morphology. This approach, founded on treatments by Raup [42], is rich and rewarding. Future functional and evolutionary morphologists will increasingly focus on constraints [40, 43].

There is not a limitless array of forms, and I believe that functional and evolutionary morphologists could make a major contribution if they were to focus on the reasons that forms and functions are "clumped" instead of dispersed [28, 44]. There have been many attempts to study this problem [27, 45]; the most promising are those that focus on form as the principal factor to be explained rather than as something that will enable us to study some other process.

One example illustrating my case is convergence and parallelism. These phenomena are studied in the field by individuals such as ecologists who want to demonstrate the degree of perfection of a particular case of convergence [46]. The original observation of similarity of form (often very simply determined—two species "look alike") is used to hypothesize similarity of biological role, and the worker might predict similarity in feeding habits. If these habits are not found to be very similar, the worker returns to the morphology and may find that the animals being compared were only superficially similar. But to me convergence is fundamentally a form concept. Two unrelated organisms are convergent if they have the same or closely similar form; this form likely will function similarly (function here is simply activity of the animal). But performance in an ethological or ecological context is neither assumed nor necessarily expected from my point of view. What needs to be explained in the case of convergence is how two unrelated organisms have come to have essentially the same form. When morphologists seek to answer the other questions, I believe that they dilute their approach and lose sight of what should be the primary objective.

A final area of investigation that I believe deserves much more attention than it has received is the rate at which morphological change occurs. I refer in particular to major morphological features, or key innovations. These have been studied by a number of modern functional morphologists [47–50], but only rarely is an attempt made to analyze how rapidly the particular adaptation has arisen. One approach has been to attempt to estimate the minimal number of genetic changes that might have been necessary for a particular morphology to have appeared, and then simply to assume that standard population genetic methods could be applied. This approach was used in the highly stimulating work by Davis [22] on the evolution of the giant panda. The role of heterochrony in rapid or saltatory evolution has been explored for over a century, but there is a recent rebirth of interest in this area. Several useful examples exist of methods of analyzing complex morphologies that could have evolved rapidly [41, 51, 52]. I advocate use of these methods, but advise complementing them with biochemical and immunological approaches [53]. There are strong reasons for assuming that rates of biochemical and morphological evolution are largely independent [54, 55]. I believe that biochemical evolution proceeds in a much more regular manner than does morphological evolution, and thus biochemical comparisons between taxa can be used to provide rough approximations of time since divergence from a common ancestor. By developing matrices of biochemical or immunological genetic distances and comparing them with existing taxonomies based on morphology one can estimate time required for certain morphological features to have evolved [53]. With this information one can then probe into history and attempt to determine the kinds of genetic and developmental processes responsible for the evolutionary event to have occurred. I would expect a full range of rates, from very slow to very rapid, just as we discern in general in the fossil record. But the fossil record is not only woefully incomplete—it also requires morphological interpretation, and I do not see how one can use the fossil record to tell us much about rates of morphological change except in unusual circumstances [56]. Biochemical methods provide an independent assessment of both evolutionary relationships and time, and thus are less inherently circular than are those based on morphology alone.

Morphologists have much to contribute to modern biology. I believe that our contribution would be greatest if we focus sharply on the central concern—the evolution of form and its function—rather than trying to be "useful" to various associated disciplines. In order to understand the evolution of form and function, it will be increasingly important for morphologists to work as developmental biologists, biomechanical engineers, mathematical biologists, molecular biologists, and even population and community ecologists. Not for a moment do I advocate departing from morphology to these areas. Rather, I believe that instead of making morphology relevant to these areas, it is morphologists who must take the lead in making neighboring disciplines relevant to morphology.

A recent, stimulating paper demonstrates the highest level of natural selection ever measured in vertebrates [57]. Large-beaked members of a species of Darwin's Finches had a strong advantage over others during a period of intense drought, for they were able to open large seeds that came to predominate as the drought progressed. While morphological literature was cited in passing, the only morphological data presented were simple multivariate statistics of external bill dimensions. The study was conducted by ecologists; we need such studies conducted by morphologists, who would then delve into the genetic and developmental basis and functional significance of the morphological differences among individuals and apply these results to morphological studies of the adaptive radiation of this group of finches [58]. Here is an outstanding opportunity for making ecology and genetics directly relevant to the evolution of morphology. Arnold [59] has recently devised an analytical method for studying selection for morphological adaptation. This method, based on quantitative genetic theory, involves measuring selection on morphological traits in two steps: first, by measuring the effects of morphological variation on performance (by direct laboratory investigations in functional morphology), and second, by measuring the effects of performance on fitness (ideally, in the field). Arnold's suggestions, too detailed to present here, involve a difficult research program and only partial estimates of selection will be derived; but we must have such studies if we are to gain an understanding of the force and role of selection in the evolution of morphology [60]. At present there are no adequate studies in this important area.

Conclusion

Functional and evolutionary morphology is a new field that has largely emerged in the past 25 years. It is founded on great traditions, but the goals are different from those of the comparative anatomists of the past (with some notable exceptions, for example, Davis). Yet, despite the enthusiasm and dynamism of recent years, there is cause for concern. No central principles have as yet emerged, and there are few, if any, commonly accepted long-term goals. Many parallel tracks are discernible, but there is little or no cohesion to the field. Subdisciplines are expanding without interlocking. This concerns me, but I am optimistic. I think that the holism advocated by Dullemeijer demands so much as to become ultimately defeatist, and few share either his philosophical orientation or prowess. On the opposite extreme, neither does the future of the field lie with the cladists, for I believe that the proponents of cladistic orthodoxy, with their insistence that no value judgments be made concerning morphological "characters," are fundamentally at odds with functional and evolutionary morphology. They, too, are ultimately defeatist, I believe.

I advocate that morphologists seek their own evolutionary explanations and not be content to provide grist for the mills of others. What is to be explained is why there are so many kinds of animals, why they have so many forms, and why these forms function in such diverse ways. But perhaps an even more important corollary is—Why are there not *more* kinds, forms, and functions? The nature and causes of limits to morphological diversity will be determined by morphologists alone, but in order to probe these matters they will need help. In this respect I foresee the continuation of the current healthy trends in biomechanics, development, and the newly emerging subdiscipline of ecological morphology. By incorporating experimental approaches and solid theory, and by making the comparative method ever more sophisticated, morphologists will continue to occupy a center stage in modern biology. Some of our best students are drawn to this functional and evolutionary morphology because of the compelling and self-evident importance of the central concern—the explanation of form and function in an evolutionary perspective. In contrast to the situation prevailing a quarter of a century ago, the future appears bright.

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