Architecture in Living Structure

Edited by G.A. Zweers and P. Dullemeijer

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Proceedings of a symposium on

Architecture in Living Structure

The primary goal of the symposium was to arrive at a comparative analysis of various methodological pathways.
The symposium was organized by W.F. Gutmann, P. Dullemeijer and G.A. Zweers and was held from March 15-17, 1984 in the Lochmühle, Aussenstelle der Senckenbergischen Naturforschenden Gesellschaft, Frankfurt am Main.
This issue is edited by G.A. Zweers and P. Dullemeijer.

Contributions to the symposium

Additional symposium presentations

W.J. Bock: Parts and wholes in morphology: a reductionistic and integrative approach to holism.
W.J. Bock: Adaptations and other structural components to fitness.
W.F. Gutmann: Organisms as energy converting systems.

Symposium participants

R. McNeill Alexander, J. Bereiter-Hahn, J.C. Vanden Berge, W.J. Bock, Tj. de Cock Buning, P. Dullemeijer, A. Grosse-Lohmann, M. Grasshoff, W.F. Gutmann, U. An der Heiden, W. Maier, J.W.M. Osse, E. Otten, D.S. Peters, G. Rehkämper, W.E. Reif, E. Reisinger, G. Roth, K. Vogel, M. Weingarten, E. Zeiske, U. Zeller, G.A. Zweers.

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DIVERSITY OF FUNCTIONAL MORPHOLOGICAL EXPLANATION

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An introduction to the 19th Lochmühle conference on 'Architecture in living structure', organized by P. Dullemeijer, W.F. Gutmann and G.A. Zweers, held from March 15-17, 1984 in the Aussenstelle des Forschungsinstituts Senckenberg der Senckenbergischen Naturforschenden Gesellschaft, Frankfurt am Main.

1. INTRODUCTION

Although functional morphologists form a minority group amongst biologists, there is, among them, a wide diversity of opinion in approach, aim, attitude and procedure, resulting in controversial questions and answers.

This Lochmühle conference was organized to elucidate these differences with the aim to obtain a soil for a mutual understanding. A first prerequisite to reach this aim is an analysis of the various motives to do functional morphology and the applied methodologies. Therefore the participants were asked to emphasize the following aspects:

1. to indicate the aspects intended to be explained in a functional morphological case study;
2. to clarify the type of explanation;
3. to describe the subsequent methodological steps;
4. to focus on the following questions:
   a. how the conclusion depends on the first step of abstraction;
   b. how the conclusion changes if the selected part is considered a member of an integrated wider system;
   c. how the conclusion and the procedure changes when temporal aspects, such as ontogeny and evolution, are introduced.

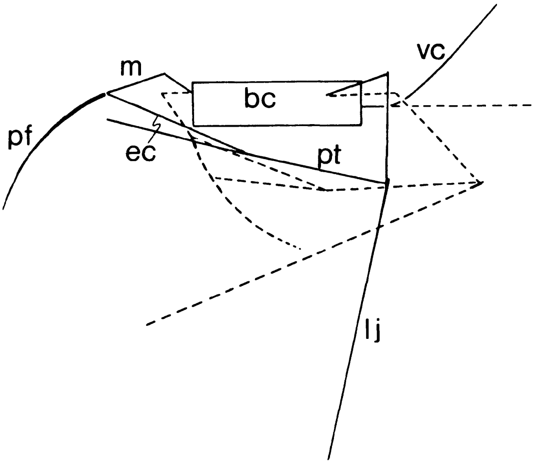

Figure 1. Diagram of the bony elements in a viperid snake. Drawn lines: opened mouth; stippled lines: closed mouth. bc, braincase; ec, ectopterygoid; lj, lower jaw; m, maxilla; pf, poison fang; pt, pterygoid; vc, vertebral column.

1.1. An example

As an introduction I shall demonstrate the various possibilities of explanations on a very simple, almost classical example, rather than present an abstract discourse on philosophy, procedure and science theory [5].

There is a small bone in the upper jaw of a viperid snake (viper, rattlesnake), the ectopterygoid, which transfers the force and movement of the protractor and levator pterygoid muscles to the maxilla (fig.1). As a result the latter is rotated so that the poison fang is erected. The ectopterygoid is retracted by the adductor pterygoideus muscle. This mediation of protractor and retractor movement during strike and swallowing is its function, its biological role, in a total chain and pattern of structures and movements. To fulfil this role the bone has to perform certain activities; one of them is to resist the strain put on it. Evenly distributed strain resistance of a specified bone is obtained by a specific shape, given the kind of material. This statement is reasonable in view of general experience from engineering science, but it needs of course an accurate analysis in each particular case. This analysis is provided by the deductive method, by which the shape is deduced from the functional

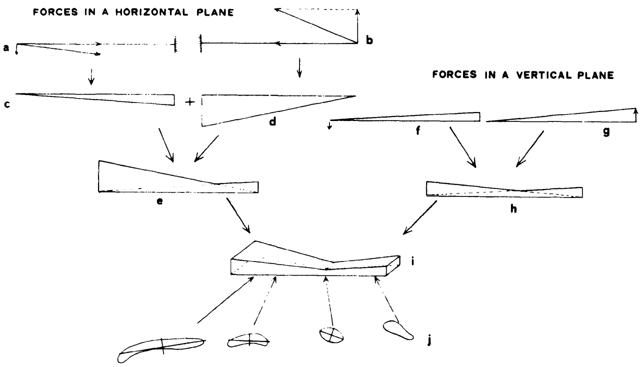

Figure 2. Mechanical model for the explanation of the shape of the ectopterygoid in *Vipera berus*. Left row the construction of the model for the activities of the muscles in retraction (a) and protraction (b) in the horizontal plane. In (c) the necessary shape for resisting the bending and compression for the retractor (m.adductor pterygoideus), in (d) that for the protractors (m.protractor et levator). As both systems work alternately, in the addition both figures can overlap (d). In (f), (g) and (h) the same in the vertical plane. Combining (e) and (h) results in the three-dimensional model (i), which is compared to the actual shape represented by cross-sections.

demands by means of a general theory (fig.2).

In this deduction the following steps are taken [6] .

1. Of all functional demands the resistance against muscle force is selected.
2. The position and the length of the ectopterygoid in the construction is taken as a given feature.
3. The type of construction is determined.
4. It is supposed that the elasticity of bone is known and that the material is evenly distributed.
5. It is supposed that the laws of static mechanics are applicable.
6. A model of the shape is made by applying the principle of optimal design.
7. The model of the shape is compared to the actual shape; the model is accepted or refuted.
8. If accepted it is concluded that the shape is explained from the functional demand (*i.e.*, the activity of the bone) by means of the theory of statics under the mentioned boundary conditions.

In formula S = f(A) in which S = shape, A = activity and f the explaining theory. This is the general deductive-nomological formula of Hempel and others [9]. In Popper's system the falsification of the models is emphasized [12], whereas in other systems confirmation is accepted, as is common in the majority of natural sciences.

2. TYPES OF EXPLANATION

If we now generalize this formula in Hempel's sense as y = f(x), in which y is the phenomenon to be explained (the explanandum) and f(x), the explanans, of which f is the explaining theory and x, the explaining phenomenon, we can use it to demonstrate the differences in morphological explanation.

As morphologists we shall always take for y a morphological feature. However, for x we have many options: the activity, another form feature, a completely different phenomenon, *e.g.* an ecological factor or a behavioural aspect [14]. As the latter two pose the demands for the whole animal, we recently have divided functional morphology into ethological and ecological morphology. We also distinguish a 'bauplan' morphology, be it that this term does not cover the original idealistic 'bauplan' concept but the concept of totality composed of interrelated functional components, *i.e.*, constructional morphology [3,7].

For f we can also introduce different factors. In the example I used a mechanical theory, but other physical theories (such as optics) as well as other theories from biology itself such as selection theory, evolutionary theory, morphogenetic theories, can be used. Whether we still want to call it functional morphology is a matter of taste, as long as form features are explained and the various explaining formulae are not mixed.

If activity and shape are reversed in position we generally are dealing with a physiological explanation. However, the reversal is also met in morphology to analyse the biological meaning of a structure. The conclusion reads then that one understands the form feature because it fulfils an essential activity. So, although in practice the reversed order is used, the ultimate logical formula is the same. Although there are striking examples of confusing explanatory principles in biology, within the theme of our conference other aspects of the procedures are more important for the understanding of the differences in opinion. In the example we observed a functional explanation of the shape by means of a mechanical theory and we can ask now whether other explanations of the shape are possible.

In addition to the functional explanation we may try a causal and a historical explanation. If we do so we see a peculiar shift in the choice of the parameters. A morphogenetic or causal explanation of the shape means that we try to find the factors influencing the origin or the change of shape. In the latter case the known phenomenon should also be a shape, be it at an earlier stage, and f must be the theory describing the process of influence. So we lose the activity of the bony element, whereas the forces of the muscles appear as causal factors in the theory instead of structure-demanding factors. Notwithstanding the fact that the statement: 'the shape of the bone can be derived from the demands put on it by the muscle forces' seems almost identical to the statement: 'the shape of the bone is influenced by the muscle forces', both explanatory formulae are quite different. It is therefore not allowed to equalize both explanations, but only permissible to transpose one into the other with additional information, *i.e.* bone is sensitive to force influences in such and such a way, so that the parameters in the explanatory formula shift.

We observe a comparable shift when we go from a functional explanation to a historical one. However, the historical explanation has more aspects. There is first the historical sequence, obtained by comparing various ectopterygoids. Then x is the first member in the sequence, y the following, and f the theory of comparison. This sequence can be set up as a purely morphological, *e.g.* in idealistic comparative or formal morphology. Another, more appropriate way for us, would be to construct a sequence of functional components. If combined to muscle force we get a combination of the functional explanation with the sequence explanation. The functional complex, *i.e.* the result of the functional explanation, is described in x as the first member, and y as the second member, and f is the theory of comparison. In other words, the change of the demands is related to the change in shape with the same explanatory theory.

A particularly interesting situation is the scale effect [1]. In most constructions the proportions of demands and shapes are non-linear and the shape has a limited size increase due to the boundary conditions. The result is that sudden changes in shape can occur with a linear increase of the demand. This phenomenon is even more apparent when more than one demand has to be met, because even with linearity of each demand they do not have the same linearity. The sequence of demands and shapes is often recognized immediately and taken as the beginning of an investigation. We are dealing then with an inductive methodology, in which primarily a relation or correlation between demand and shape is described and, thereafter, a theoretical explanation is suggested. Such a sequence does not (yet) give any insight in the causes of the changes.

Another step is therefore to introduce causality, as in morphogenesis, but then placed in its historical context, in other words, the change of the developmental process and result during history and, last but not least, causality as formulated in evolutionary theory in terms of mutation and selection. The latter two steps need further exposition.

Here I like to add a few words on the concept of adaptation in order to prevent confusion. This term is used for all the connections of y and x, so that we have a means to distinguish the various meanings of this concept. It is used for the connection activity-shape, for function-shape, for environment-shape (in the case of the example of the bony element, the environment is the muscles), for morphogenetic change, for the measure of selective value, for evolutionary change.

3. FURTHER METHODOLOGY

Returning now to the example we can ask a number of questions relating to the methodology. First, why did I choose this bone and focus only on the shape. For this presentation I used it as the simplest case in which I can demonstrate easily the methodology. However, more important is that this bone is a member in a chain of elements assembled in a complicated construction, a totality. This, in principle, holistic point of view is the most important starting idea for functional morphology. Structures, components, elements, or whatever they may be called, must fit together to form a meaningful construction, a system, symbolically a pattern or network, and frequently bound to a specific space. In this view an element cannot be understood without taking into account its membership in the totality. Whether this totality concept is the same as the machine concept [8] depends on the definition of the machine concept. If the latter is taken very broadly including not only kinematic and chemical processing, but also production and reproduction, and if the machine parts are considered changeable, then an analogy is possible. However, it is doubtful whether the machine concept needs to be used instead of the organismic, structuralistic or holistic concept which seems to encompass the machine concept (cf. [4]).

The fitting together of the structures, components and elements can also be formulated as a mutual demand although it is different from the functional demand. The former relates mainly to space, position and size features, whereas the functional demands require generally position, form and structure features. The theories in the explanatory formula are the rules recognized in architecture and construction sciences (constructional morphology!) and contain various aspects as functional, behavioural, ecological components. Whether all these aspects should be called functional is a matter of how wide one wants to define function. Although some of us are working on these aspects, little is still worked out theoretically (the idea of capsular matrix of Moss [11]; the simple concept of mutual exclusion in space; the positions in a chain of rigid elements; the positional aspects of muscular attachments).

In Roux's idea [13] space occupation was morphogenetically a matter of mutual force and strength (Kampf der Teile); a struggle between the elements. This seems to be so in cases of diseases, but in general there is a rather strict programming of the space occupation with an order in dominance.

Particularly interesting is the combination of the two types of demands, shortly called the functional and the spatial demand (including topography, size), leading to systems showing all kinds of compromises, integrations and additions, which can shift under the influence of minor changes in the demands and their proportions.

4. THE SELECTION AND ABSTRACTION

It is evident that a totality cannot be explained at once. At best we can say that we understand (verstehen) the totality, that we have an intuitive comprehension but not (yet) an explanation in the deductive sense. Therefore a selection of features is made using this intuitive understanding by selecting what one 'believes' is the dominant feature. There is no proof of the relevance of this selection except for the *a posteriori* conclusion that it works. From thereon the relationships between the members in the totality can be established. I want to stress the point that the members are *distinguished* for analytical purposes, but that they are not *separated* from the totality.

Various investigators will have different opinions on what they think are the dominant features; it depends on the problems they are interested in, their personal taste and the criteria they use for the selection. For us the totality consists of a number of more or less dominant components, the main functional components or systems (*e.g.* Gutmann's hydraulic system, [8]). Such a view-point of course influences the entire procedure, the choice of the methods and technics, and has effects on the type of conclusion to be reached. It may well be that somebody else, although working with the same animal and the same elements, reaches a completely different conclusion when the goal of the research is set differently.

If the choice of the component is already a strong selection from the total construction, this is even more so for the selection of the features of the component. In the example only the shape of a bony element was explained and that only partly and approximately. Other features as position, size, structure and many details were left out of consideration. The same holds for the demands supposed to be significant. Here again is ample opportunity to reach different results and the interesting problem arises how these differences can be connected, a necessity to approach the ideal of completeness in the explanation. The features or properties of interest are not always selected on purely functional anatomical grounds; frequently we see investigators with a different goal in mind, yet calling themselves functional morphologists, using analogous choices and strategies. It needs no further argument to see that most likely they do not agree on the explanation.

In this volume many contributions treat other structures and other features of these structures. If so, they certainly will use other explanatory theories. *E.g.*, I expect that the hydraulic theory is used when position and presence are explained, but when it comes to size, shape and structure of the composing elements, hydrostatics and rigid body statics must be applied. In case of sense organs, optic and acustic theories are used, and in respiratory organs, physico-chemical theories of diffusion, aerodynamics, *etc.*, are useful.

5. APPLICABILITY OF THE THEORY

How can we check the applicability of the theory if the theory cannot be falsified? This is indeed a difficult problem which I can demonstrate also on the ectopterygoid example.

If the theory as such cannot be falsified, we must rely on other methods:

1. When we frequently see that the relation is falsified we may become suspicious, but never can be sure that the theory is not true.

2. We can sum up all the preconditions which have to be fulfilled to allow application and then try to get some 'feeling' how far these preconditions are met in the biological phenomena. If they are met and the relation does not hold, again we can begin to distrust the theory.
3. We can try to make an analogy, *i.e.* see whether the observed structure shows features which can be compared to physical entities of the theory and then become suspicious if the theory cannot be used.

In the example I used simple statics supposing that the bony material is homogeneous and evenly distributed. In a rough approximation it works but neither the composition of bone nor the analogy gives us a legal argument to apply this simple type of mechanics. Bone is adapted by arrangement and proportions of its composing material which moreover may be chemically different from locality to locality. We need therefore the mechanics of composite material for which the theory is hardly developed. Secondly the bone may be constructed not primarily to withstand static strains but serve to absorb energetic effects.

I could present a long list of discussions and disagreements in the literature which all can be reduced to this kind of theory choice. Most striking was the well-known pre-strained concrete model by Knese [10]. The question is not without practical importance because much medical treatment and surgery was founded on these theories. However, in most cases as in the mentioned one, the theory was never falsified; it could only be concluded that the wrong theory was applied.

6. FALSIFICATION OF THE EXPLANATORY THEORY

In the foregoing I stated that only the explanatory relation could be falsified and not the constituting parameters. Although this statement is generally accepted among science theorists, in practice many investigators do not follow it and much discussion is going on whether some theories are true or not. This may be a false discussion, but more likely the situation and understanding of the falsification problem is more complicated in natural sciences than the strict simple logical derivation.

If the relation does not hold then there is the possibility that

1. one or each of the terms in the formula is incorrect;
2. the criterion of comparison is incorrect, *e.g.* non-comparable parameters.

Biologists tend to believe in the correctness of their observations. That implies that the incorrectness of y is ruled out. However, the observation may have been with a preconceived idea, so that a biased presentation is presented, although this generally will not be the case. The second possibility can easily be corrected by a careful considering of the conditions and parameters to be compared. We are left then with the possibility that x of f, or both, are incorrect. The incorrectness of x would imply an incorrect observation or a selection of observed parameters which were unimportant or irrelevant for the explanation. This happens when investigators are convinced that certain parameters are more important than others, *e.g.* in my example I was convinced that static loading is the most important factor determining bone shape. It could have been that this factor was of minor significance or even irrelevant. Again it is very unlikely that such a wrong supposition or observation cannot be corrected, although in complicated situations long lasting discussions can go on, *e.g.,* discussions about the causes of diseases or, for bone, the factors effecting bone growth.

The possibility remains that the theory is incorrect. A common attitude in most discussions is that this implies that the theory as such is incorrect or that the theory is untrue. This need not be so; on the contrary, generally there is a wrong *choice* of theory. The falsification of the relation cannot be used as a proof of incorrectness of the theory. I shall not prove this but only illustrate it in our example. In this example I applied the theory of statics. When we look at the comparison in much detail and very precisely, it can be said that the relation does not hold. What happened is that we needed the theory of composite mechanics. This does not prove that the theory of traditional statics is incorrect.

There are other methods to test the correctness of the theories. In the case mentioned we left this test to our colleagues in physics and trust them, the more so because it can be shown that the conditions to be fulfilled to apply the theory were not met. Only when these conditions are met and still frequently the relation does not hold, is there a reason not to trust the theory. In these cases one speaks of a paradigm change, which is something different from when the basic philosophy changes (*e.g.* from idealistic to realistic philosophy, which is also a kind of paradigm change).

Until now there has been little reason to doubt the theories borrowed from physics and chemistry, but how about the biological theories. There we have to test the theories ourselves. Biological theories vary considerably in preciseness and general applicability. Many of them, and among them the most important ones, are not only constructed from exactly determined observations and strict logical or mathematical relations, but contain a large quantity of possibilities, most likely suggestions, and so on. The concepts are frequently ill-defined or cannot be used generally. The consequence is that not only purely logical theoretical concepts and relations are included in the theory, and thus discussed, but that a good deal of the observations of particular cases and 'surrounding' phenomena are presented simultaneously. Such discussions are generally senseless if a careful analysis of the correctness of the constituting elements and their relations in the theory is not made.

To test a theory there are basically two methods: axiomatising, to which belongs an analysis of logical consistency, boundary conditions and extensibility, and generating of hypotheses, in the sense of prediction of phenomena, which can be tested.

The use of theories brings us to the following step: the testing of the model. If correctly done, the criteria on which to decide on falsification or acceptance of the model should be set independent from and before the comparison. To begin one tends to set these criteria rather loosely and gradually increases the rigidity or acuteness of the criteria.

In the example we began to be satisfied with a rather general concurrence between model and reality and tried to add subsequently more and more details. Addition of these details may consist in adding new demands, reconsidering the boundary conditions, taking refinements of the theory, taking into account more detailed assumptions underlying the theory, refining the observations and adding new features. This is also the procedure when a model is not in agreement to the reality. Then all these factors may be improved by an iterative method. Again these aspects may lead to discussion points.

7. OPTIMAL DESIGN

One reason for disagreement, frequently heard, may be the inadequacy of the application of the principle of optimal design. Indeed, the only way to arrive at one or a few models is to apply such a principle, whereas otherwise anything imaginable could serve as a model. Using it in this way is not more than a necessary method. However, somewhere optimal design needs also some basis in the biological reality. Would this not be the case then we would find hardly any case of agreement. It has been supposed in general that optimal design is not unlikely to occur in view of the cost of energy, material and survival strategies (*cf.* [2]). Whether in certain surroundings living creatures can allow waste of energy or material is to me an open question; it will be impossible to prove this in view of our axioms and with the procedures used in natural sciences.

The problem is how to recognize those suboptimal situations which do not result from compromising. Practice is that when we find such a situation we are bound to draw the conclusion that we have to improve the model as I mentioned before on the penalty that our entire explanatory system in biology will break down. The escape is generally that we allow sometimes a temporary suboptimal situation, *e.g.,* in ontogeny or certain stages in phylogeny, simply because we do not know better and suggested as it is by the application of the optimal design. A suboptimal situation would imply that at least a part of a feature would be functionless, which is very difficult, if not at all impossible, to prove. If one of the attributes or properties is taken as a part of a feature, non-functionality may refer to so-called irrelevant properties [6] . In the case of the example, the weight, which the bone has as a consequence of its size and shape, is functionless. However, we can never be sure that we did not miss an essential demand, even more so, the demand may be ultimately coincide with the activity the organism can perform with its structure. In view of the methodology this cannot be discovered; it points to an unavoidable circularity in the methodology of the investigation of the form-function relationship. Thus there is all reason to believe in a certain circularity in our reasoning, but not worse than we find in mathematics and other natural sciences. During our circular stroll we can gain a lot of insight in the structure of nature. Thereby it is of paramount importance that investigators make their methodology and their basic philosophy clear be it sometimes in an implicit way. And this is what has been asked from the contributors of this volume, so that we can obtain some insight in the differences of opinions and conclusions.

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PRINCIPLES OF SELF-GENERATION AND SELF-MAINTENANCE

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ABSTRACT

Living systems are characterized as self-generating and self-maintaining systems. This type of characterization allows integration of a wide variety of detailed knowledge in biology.

The paper clarifies general notions such as processes, systems, and interactions. Basic properties of self-generating systems, *i.e.* systems which produce their own parts and hence themselves, are discussed and exemplified. This makes possible a clear distinction between living beings and ordinary machines. Stronger conditions are summarized under the concept of self-maintenance as an almost unique character of living systems. Finally, we discuss the far-reaching consequences that the principles of self-generation and self-maintenance have for the organization, structure, function, and evolution of single- and multi-cellular organisms.

1. INTRODUCTION

Are there properties common to all living beings that distinguish them from non-living beings? In view of the enormous richness of forms and structures developed in the realm of the living on the one hand, and of the increasing success in reducing many processes in living systems to physico-chemical relationships on the other, both an unambiguous delimitation of the living from the non-living and a common characterization of all living beings appears to be a futile endeavour from the very beginning.

Nevertheless, each of us cannot deny the feeling, that in general there is no problem in deciding whether or not a given thing is a living being. Is a justification of this feeling possible by specifying some criteria with scientific scrutiny, thus allowing a clear distinction? Or are living systems only gradually distinguished from non-living systems by their degree of complexity? In the latter case we can never fail by investigating living systems just like others. However, if the first case holds, then it may happen that, even if all our scientific investigations are correct, neglectance of these criteria may exclude a comprehensive, profound insight into the special nature of living beings as well as the development of concepts unifying the mass of details in so many fields of biology. In fact we all suffer from the abundance of specific knowledge accumulating in many special areas.

In our opinion there are principles of organization shared by all living beings which are realized neither in natural non-living systems nor in artificial systems up to now created by man. Such principles are stated and derived here. For a more detailed discussion the reader is referred to [6].

2. PROCESSES

We start with the observation that the physico-chemical world has a structure consisting of spatially and temporally related events. Any spatio-temporal domain which in some way is separated from its (spatio-temporal) environment is called a *process*. A process can be characterized by a connected four-dimensional spatio-temporal domain B and certain physico-chemical entities or quantities V1, V2,..., Vn occurring in this domain. These quantities are comprised into a vector V = (V1, V2,..., Vn). *E.g.* V1 might be an electric field, V2 a magnetic field distributed in the domain B. Or V1 might be a distribution of mass across B. Some of the components of V could represent concentrations of certain types of molecules existing in B. (For simplicity we do not consider here problems of description connected with quantummechanic and relativistic phenomena. However, these may be accounted for without changing the theory essentially.) Note that connectedness of B implies connectedness of the time domain T of the process. For each point of time t from T the (three-dimensional) *shape* or *Gestalt* Bt of the process is just the restriction of B to that value of t. It is not necessary that Bt is a connected set in three-dimensional space.

The separation or delimitation of a process P = (B,V) from its environment consists of two parts: spatial and temporal delimitation The two-dimensional spatial delimitaion at a moment t is given by a steep (eventually discontinuous) spatial gradient of at least one of the intensities V1, V2,..., Vn. In this way the spatial boundary dBt at time t of the process is defined not numerically precisely but identifiably. *E.g.*, it may be given by a steep gradient of the concentration of some type of molecules.

Temporally a process starts in one of three forms: either from several others by fusion or by division of a previous process or by the building-up of a new steep spatial gradient separating the new process from its environment. Correspondingly a process ends by dividing into several others or by fusion with some others or by smoothing of the steep gradient defining its spatial boundary. In this way also the temporal boundaries of a process, its beginning and its ending, are identifiably defined.

In a broad sense the *environment* of a process is everything outside its domain B. However, due to the principle of nearest action only those conditions of the environment that actually meet the boundary of the process can have some effect on the process. These conditions decompose into the *initial conditions* given by the state of the world in the neighbourhood of the place where the process starts, and into the *boundary conditions*. For each time t of the process the latter are given by the limit values of the intensities *external* to the process observed at the spatial boundary dBt.

Examples of processes are: stones, waters, the earth, cells, organs, organisms, molecules, machines, chemical reaction systems.

3. SYSTEMS

Any process may be considered as a system with *components* V1, V2,..., Vn. However, more generally we imagine systems whose components are processes. To this end we define two processes P1, P2 to be *disjoint* if their domains B1, B2 have in common only boundary points. Two disjoint processes P1, P2 *interact* if they come into contact at some time, *i.e.* if there is at least one time t at which they have parts of their boundary in common (not necessarily fusing). A *system* S is a union of mutually disjoint processes P1, P2,... satisfying the condition that any two of these processes are connected via a chain of interactions within this set of processes. P1, P2,... are called the *constituent subprocesses* or the *constituent parts* of the system. Subprocesses of constituent subprocesses are examples of nonconstituent subprocesses.

Machines are examples of systems. However, in order to define a system properly it is necessary to specify which parts of the system form the constituent parts. Normally these will not be the molecules, but some macroscopic objects (which are also processes in our sense). *E.g.*, in a mechanical clock these may be the cog-wheels, springs, and casing. Considering the molecules of the clock to be its constituent subprocesses would define another system.

There is another problem in defining a system. No one would call a set of cog-wheels, springs, and casing a clock when these things are lying disconnected on the table. Generally also a certain set of relations between the constituent parts have additionally to be specified in order to define a system completely. The relations defining a system are called its *constituent relations* (there are generally many more relations in a system, *e.g.* relations between non-constituent subprocesses are non-constituent relations). Hence a system is defined by a set of constituent subprocesses *and* a (possibly empty) set of constituent relations between these subprocesses. Therefore the existence of a system is not only bound to the existence of its subprocesses but also to the satisfaction of its constituent relations. Only in this way it is possible that constituent parts of a system may exist before or after the system exists, namely before or after the constituent relations are satisfied.

With machines it is generally the case that its constituent parts exist already before the machine exists. Building a machine not only requires building its parts but also constituting certain relations between these parts.

4. SELF-GENERATING SYSTEMS

An essential point of this paper is to show that the constituent parts of a system do not necessarily exist prior to the system. This observation leads to the concept of self-generating systems which produce their constituent parts by and within themselves, and moreover, constitute the relationships between these parts by themselves.

In an absolute sense a system cannot generate itself. If it has an origin, this origin must exist before and outside of it. Each originating system has a history determining its initial condition. However, the notion of self-generation attains a realistic meaning by the following definition: A system is called *self-generating* if there is some time of its existence after which it contains only constituent subprocesses originating within the system. "Originating within the system" means that the initial conditions of the corresponding subprocess are constituted at least partially by other constituent subprocesses *belonging to the system.*

Examples of non self-generating systems are machines composed of parts. These parts do not display the property of participating in the generation of the other parts of the machine. Whereas in non-self-generated systems the parts exist independently of the system, in self-generating systems the system is a condition for the existence of its constituent parts, at least after some time.

Examples of self-generating systems are chemical reactions in the course of which all reactants are newly formed. Most remarkable in this context is the well-known Belousov-Zhabotinsky reaction, where in a cyclic fashion new substances (which may be viewed as the constituent parts) are permanently synthetized. Other examples are populations consisting of individuals as subprocesses connected by a network of descent. When we look at multicellular organisms there are many ways to decompose them into constituent parts or processes. One way would be to consider the organs as constituent parts, a second one the cells, a third one biological macromolecules, finally atoms and elementary particles. In a strict sense another system is defined each time (despite the fact that in all cases the same "whole" is given). If the lowest level, the atoms and elementary particles, is chosen, then the system is not self-generating, since in this case the constituent parts exist before and independent of the system. However, if the organism is conceived to be composed of its organs then clearly these constituent subprocesses are generated within the system, and in this respect the organism is a self-generating system. The same result holds if the cells are defined to be the constituent subprocesses.

At this point it becomes clear that to say an organism is nothing else than a complicated machine may be misleading. Organisms are self-generating systems whereas machines are not (at least those existing up to now). It may even be the case that there are rather simple self-generating systems and on the other hand rather complicated machines which are not self-generating (*e.g.*, sophisticated computers).

5. SELF-MAINTAINING SYSTEMS

With respect to life the fundamental question arises how its process was able to persist without interruption for a period of several billion years under a tremendous number of destructive environmental influences.

The notion of self-generating systems opens the view on systems that show the property of outlasting their own parts or subprocesses. Normally a system perishes together with its parts. This is the fate of all machines having existed so far, if their parts are not exchanged. Likewise it happens with all non-self-generating composite systems. Sooner or later they disintegrate because of influences of the environment or internal fluctuations. But also most self-generating systems cannot persist forever. *E.g.* chemical reactions generally terminate after several reaction steps in a state of local thermodynamic equilibrium. But if there remains a steep gradient separating the system from its environment the system must disintegrate although this can take place very slowly, *e.g.* in the case of a solid system at low temperatures. Only in the exceptional case that conditions of coexisting phases are fulfilled precisely, a spatially limited system can persist in full thermodynamical equilibrium. But even in this exceptional case, maintenance is quite different from our concept of self-maintenance. Self-maintaining systems, as we define them here, are not in a state of thermodynamic equilibrium, and nevertheless persist in principle forever.

One could imagine a machine persisting for ever in the way that each of its parts is repaired again and again or replaced by new parts. But obviously such a machine needs other systems that perform the repairs and replacements. Thus the problem of maintenance and persistence is deferred to these other systems. Essentially, a self-maintaining system is a system that can do these operations by and within itself.

A system of machines that repair each other in a way such that they altogether persist would be a self-maintaining system. However, that the machines, which in this case are the constituent subprocesses, persist, would be too strong a postulate in our context. We only require that the system as a totality persists, whereas the constituent subprocesses may come and go. *I.e.* we imagine a system of machines which persists indefinitely despite the fact that the individual machines do not necessarily persist within the system. Of course when individual machines permanently stop existing or are brought out of the system, then maintenance of the system requires that new machines are built permanently.

Moreover, we do not postulate that repair of a machine or construction of a new machine always leads to the same type of machines. We allow series of repairs that may transform the machine drastically. Of course in normal language one would not speak of "repair" in this case. If we would only allow repair and replacement in the sense of exact restitution of a previous state then evolution of a self-maintaining system would be impossible.

We must also abandon certain teleological aspects in the word repair. Moreover, the term machine has to be replaced by constituent subprocess. Destruction of the machine (making necessary repair or replacement) then simply means ending of a subprocess. Repair and replacement simply mean generation of new subprocesses. Thus in a self-maintaining system there is permanent generation and disappearance of constituent subprocesses. Self-maintenance means self-generation in permanence.

The principles of self-maintenance so far discussed are summarized as follows:

(i) a self-maintaining system exists permanently in an evironment the fluctuations of which suffice to disrupt the gradient of its boundary locally

(ii) the constituent subprocesses are not in thermodynamic equilibrium with each other

(iii) all constituent subprocesses exist only for a finite time within the system, whereas the system virtually exists forever.

Virtually in condition (iii) means that permanent existence may be prohibited by one of the following factors: 1. there may occur fluctuations in the environment that are strong enough to interrupt the generation of subprocesses underlying self-maintenance, 2. condition (ii) implies that all constituent subprocesses and hence the total system will end if there is not sufficient supply of energy and matter from the environment, hence existence for ever presupposes permanent availability of energy-rich material in the environment.

The definition of self-maintenance we want to propose here is not yet complete. There are chemical reactions, like those of the Belousov-Zhabotinsky type, which under constant supply of matter and energy do not equilibrate, but periodically or aperiodically change the concentrations of their reactants indefinitely. This behaviour makes them appear fascinatingly "lively": the components come and go but the reaction as a totality persists. However, these reactions are unable to maintain the gradient of their boundary. They always take place in reaction vessels, the walls of which supply the boundary of the reactions (at least large parts of it). Without the supporting walls of the vessel the reaction would disintegrate after a short while. The vessel and hence also its walls forming part of the boundary of the reaction exist before the reaction starts. Quite contrarily the surface (boundary) of a living being does not exist before and independently of the living being. In this case the boundary of the system comes into existence just with the system itself. We take this property of a "self-determined boundary" as another important feature of self-maintaining systems and include it as part (iv) of its definition:

(iv) a self-maintaining system has a self-determined boundary, *i.e.* the boundary does not exist before and independently of the system.

All properties discussed so far are not only shared by living beings but also by populations of living beings which are connected phylogenetically. If the boundary of a population is defined as the union of the boundaries of all its individuals, then this boundary does not exist before the population, and hence it is self-determined. However, since we do not want to classify arbitrary populations as self-maintaining systems, we need another distinctive condition which does not exclude living beings. As a necessary condition we postulate that a self-maintaining system is spatially connected at each moment of its existence. By this constituent relation we mean that any two constituent subprocesses existing at a time t are in direct contact to each other or in indirect contact via other constituent subprocesses existing at the same time t.

Spatial connectedness also allows to define the unity and wholeness of a self-maintaining system. This is necessary, because otherwise both a cell within a multi-cellular organism and the total organism may turn out to be self-maintaining. To escape this difficulty we call only those systems self-maintaining which at each time of their existence satisfy the following *maximality condition:* A self-maintaining system is the maximal spatially connected unit satisfying all the other conditions of self-maintenance.

Summing up we arrive at the following characterization: A system is called *self-maintaining* if the following conditions are satisfied:

(i) it exists permanently in an environment the fluctuations of which suffice to disrupt the gradient of its boundary locally

(ii) the constituent subprocesses are not in thermodynamic equilibrium with each other

(iii) all constituent subprocesses exist only for a finite time within the system, whereas the system virtually exists forever

(iv) it has a self-determined spatial boundary, *i.e.* the spatial boundary does not exist before and independently of, but is created with the system

(v) at each time of its existence it is spatially connected

(vi) it is the maximal spatially connected unit obeying properties (i) to (v).

Remark: It follows from (iii) that self-maintaining systems are self-generating systems.

Conditions (i)-(vi) are abstract principles of self-maintenance. They do not tell which special mechanisms and arrangements of processes are able to guarantee these properties. But they allow one to decide whether a given system is self-maintaining without knowing the mechanisms underlying self-maintenance.

Indeed, it can be easily seen that living beings satisfy these conditions, hence they are self-maintaining. There is only a difficulty with condition (iii) which is in conflict with the fact that living beings generally have only a finite life-time. It can be assumed that organisms could persist in principle for ever (in a suitable environment) if they had no genetically determined mechanisms defining upper limits of their life-time. Nevertheless they generally exist much longer than their constituent subprocesses. Such systems we call "real" self-maintaining systems, whereas the definition above characterizes "ideal" self-maintenance. The definition does not exclude the aspect that we consider a single line of cells following each other from one generation to the next as a single system. If it is true that all cells existing today derive from early cells existing several billion years ago then it is justified to say that cell lines virtually exist for ever.

Another advantage of defining self-maintenance in this abstract way is that only then it becomes clear that there may be completely different self-maintaining systems. There are in fact enormous differences between different species of living systems. But it may even be that somewhere else in the cosmos or in later times on earth self-maintaining systems exist which not even use the genetic code or the cell structure to maintain themselves.

Therefore self-maintenance is not used here to define "living". However, since up to now living systems are the only self-maintaining systems on earth, this property may be used to characterize living beings. In this way it is possible to draw a border-line between biological and non-biological entities.

6. IMPLICATIONS OF SELF-MAINTENANCE

The criteria of self-maintenance can be used in conjunction with known physical or chemical laws and in conjunction with knowledge of historical conditions on earth in order to derive a great number of conclusions on the structure and organization of living systems and their relationship to the environment. This procedure nearly automatically brings into perspective many details of the living world which otherwise appear to be combined arbitrarily and at random.

Without explicit deduction (for details see [6]) we only mention some points:

(a) Living systems as self-maintaining systems have to obey certain rules of stability. Since the individual subprocesses are in a sense unstable (iii) global and macroscopic properties of organisms have to exist which are attractors in terms of system theory. This is necessary because otherwise the always present external fluctuations (i) could drive the system into a state of collapse. The attractor properties of so-called "climax processes" have been emphasized by Schwegler [11].

(b) All equilibria observable in self-maintaining systems have a dynamic nature being realized by a balance of production and destruction (this was recognized by many biologists, well known in this context is the concept of steady state or "Fliessgleichgewicht" [1]). It follows that the global structures must be self-regulated and self-organized. Examples of global properties are the number of subprocesses at a given time, the total energy content, the amount of in- and outflux of matter and energy, shape and anatomy of the organism.

(c) If a system indeed persists for a very long time compared with the duration of its constituent processes then it is not very likely that always completely new kinds of subprocesses arise. Rather it has to be expected that sequences of processes will run into (if they are not already in) circular arrangements of processes where subprocesses of the same types are generated again and again in a definite order. There are innumerable examples of circular arrangements of processes repeating themselves endlessly in living systems. We only point to the citric acid cycle and many other basic metabolic cycles which have not changed in many millions of years despite other drastic evolutionary changes. The cell cycle is another outstanding example of circular organization. Even the stasis of many species across thousands of generations can only be explained on the basis of predominant circular organization [12].

(d) The maintenance of a steep boundary gradient, damaged punctually by environmental influences (i), requires that the system operates far from thermodynamic equilibrium, *i.e.* self-maintaining systems are energetically open systems.

(e) All local parts of the system must be accessible both to the aquisition of energy-rich material and to the outward transport of energy-poor material. All voluminous living systems have very refined transport systems.

(f) There is another type of circularity in self-maintaining systems concerning the relationship between parts and whole: The whole determines the kinds and operations of the parts and *vice versa* (whereas in "normal systems, where the parts exist before and independently of the whole, the parts seem to play the major role). This is a special type of functional organization and makes living systems appearing sometimes mysterious, giving rise to theories like vitalism and some variants of holism. However, failure of such theories does not imply that biological entities can be well understood without any holistic principles or aspects. In the sense of this paper proper account of the parts - whole relationship with respect to morphology was given by Dullemeijer [3].

This remark is also important with respect to the problem of the relation between genome and organism, between genotype and phenotype. There is growing evidence that the organism does not simply receive "commands" from the genome but that also the organism regulates the genome. We cannot go into details of this problem here.

(g) It is to be expected that a theory of self-maintaining systems will shed new light on evolutionary processes. We suppose that the theory of self-maintaining systems if developed further allows a distinction between those properties of organisms which may undergo evolutionary changes and those which have to be invariant for the process of life to go on. It is very important to note that despite the enormous variety of structures and forms of life on earth there are some, though at first glance only formal, properties common to all creatures as self-maintaining systems. These properties are invariants of evolution [9] .

In spite of the formal nature of these principles their universality is reflected in the universality of some material structures of living beings. It is very remarkable that all known forms of life are coupled to the cell structure. Under this aspect it is not so much astonishing that single cell organisms are those which have maintained themselves for the longest time in the history of life, ranging to some billion years. But also with respect to all other types of organisms it is most remarkable that the cellular structure "survived" all mutations throughout (the whole of) evolution.

There are many other examples such as the citric acid cycle or the machinery of protein and nucleic acid synthesis which were conserved across a billion years. They confirm us in our opinion that self-maintenance is characteristic for the organization of the living. The importance of the circular relationships between nucleic acids and proteins for evolutionary developments was elaborated in the theory of hypercycles [4,5] .

In this context we point to a certain explanatory antagonism. In one type of explanation constancy and stability of a species are based on a selective advantage this species has to nearby relatives. In this model a species is preserved because it represents a stable equilibrium in a competitive process. This type of explanation requires the existence and permanent production of less fit individuals in order to ensure that again and again the most fit ones are selected and conserved.

In the other type of explanations the specific properties of individuals or species remain unaltered because they are properties of processes which are stable by themselves due to their internal organization. In this case, for the existence of a long sequence of generations it is not necessary that other individuals or populations of individuals with differing properties exist.

It is very important to see that these two kinds of explanation, despite their alternative character, are by no means contradictory or mutually exclusive. We believe that they are complementary to each other and that both of them play an important role in evolution. Without some internal stabilization the competitive process and hence selection could not even take place. For any theory of evolution it is crucial to distinguish between those properties of organisms which can change without violating the principles of self-maintenance and those properties which must not or cannot change. This antagonistic twin relationship can be highlighted by the paradoxical formulation "Evolution would stop if the property of organisms to produce mutants were not a stable variant".

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We appreciate very much the incentive stimulation the work of H.R. Maturana and F. Varela on "autopoietic" systems had on our ideas presented here. A discussion of the connection between their and our concepts will be given elsewhere [6] . In addition the relationship to other characterizations of living systems (*e.g.* those by von Bertalanffy and Schrödinger) will be considered there.

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ARCHITECTURE OF TISSUE CELLS
THE STRUCTURAL BASIS WHICH DETERMINES SHAPE AND LOCOMOTION OF CELLS

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ABSTRACT

Shape and locomotion of tissue cells depend on the interaction of elements of the cytoskeleton, adhesion to the substrate and an intracellular hydrostatic pressure. The existence of this pressure becomes obvious from increase in cell volume on cessation of contractile forces and from observations with ultrasound acoustic microscopy. Wherever such an internal pressure is established, it is involved in generation of shape and driving force of cell locomotion. Therefore each hypothesis on cell shape and locomotion must consider this property of a living cell. Apparently different types of locomotion depend on differences in substrate adhesion and/or cytoskeleton organization.

1. INTRODUCTION

The question how cells move belongs to one of the most fascinating and still unsolved problems of cell biology. We have a vast amount of interacting proteins which are related to shape and motility of cells. An ultimate explanation of these properties, however, must include the mechanical interactions of all parts involved.

Mechanically a spherical egg cell is an incompressible filling enclosed by a membrane. The hydrostatic internal pressure of the system is responsible for the shape of the cell. The existence of an internal pressure in egg cells is not only obvious intuitively but rather was measured by various methods [19]. In addition streaming of cytoplasm in slime mold plasmodia and amoebae results from hydrostatic pressure differences between different regions in the organisms: [e.g. 14,15,16,28,29]. The question arises which forces determine shape and locomotion of non-spherical tissue cells as fibroblasts or epithelial cells in culture. Does a hydrostatic pressure exist in these cells?

Modern immunofluorescence microscopy provides an excellent picture of the course and arrangement of cytoskeletal fibres. Their course is strongly related to cell shape and they are able to resist tension or to exert forces. Most cell biologists consider these properties sufficient for an explanation of cell shape and locomotion. It is now generally agreed upon that several factors are involved in cell locomotion [8]:

1) The presence of a contractile system, composed of actin and myosin, which produces the motive force.

2) Adhesion of the cell or parts of the cell to a substrate which serves as an abutment and allows a conversion of forces into movement relative to the substrate.

3) A cyclic turnover of cytoplasmic components, most probable actin and related compounds: formation of a more or less fluid transport phase in the cell body region or at the rear end of a cell fragment, followed by reorganization to a fibrillar meshwork at the front of the leading lamella.

It is the aim of this article to summarize evidence for the existence of an intracellular hydrostatic pressure and its involvement in the generation of shape and locomotion of cells in culture. The question is not how far these cellular properties can be explained without considering their hydraulic properties, because, whenever an internal hydrostatic pressure exists, it must be involved in any change of shape.

2. DOES A HYDROSTATIC PRESSURE EXIST IN ANIMAL TISSUE CELLS?

Evidence for the existence of an internal hydrostatic pressure is mainly derived from three experimental approaches.

1) Observing influences of varying osmotic conditions on extension of leading lamella [6,10,12].

2) Observing volume changes induced by inhibition of contraction processes by means of calcium antagonists [24] and energy deprivation.

3) Observing changes in tension of cortical cytoplasm by means of an acoustic microscope operated in the GHz frequency range [11].

The minimum structural requirement for generation of a hydrostatic pressure in cells is the existence of a (semipermeable) cell membrane and an adjacent cortical fibrillar system, which provides the cell periphery with tensile strength. The physiological condition for the existence of a hydrostatic pressure is an osmotic inequality between the surrounding fluid and the interior of the cell [18]:

$$\pi_o = \pi_c - p_h$$

π_o: osmotic pressure in the environment

π_c: osmotic pressure of the cell interior

p_h: hydrostatic pressure generated by the cell

The hydrostatic pressure acts against the influx of water. Therefore a block of cytoplasmic contraction should be followed by a volume increase due to water influx, insofar these contractions are responsible for pressure generation. This behaviour can be observed in epidermis cells after addition of lanthanum (2 mM). Cell locomotion stops in migrating cells, in fried-egg-shaped cells the volume increases. From volume differences measured by means of reflection interference microscopy [5] a contraction generated pressure in the range of $5 \cdot 10^5 N\ m^{-2}$ can be calculated [24].

In a cell homogeneously attached to a substratum, volume changes are totally expressed in changes of cell surface topography. For that reason observations have been made with the acoustic microscope, which enables to visualise surface topography as well as reflectivity, since tension at the cell surface becomes clear from interference fringe contrast, and the volume from the course of interference lines delineating the cell surface [12]. This is allowed since the factor determining the reflection of sound waves is the difference in acoustic impedance at an interface, and the acoustic impedance of tensed structures is closely related to tension.

On addition of cytochalasin D (0.5 - 2 µg/ml) a sudden loss of contrast takes place in 2-4 min, which is followed by an increase in volume. Cytochalasin D causes rupture of the cortical fibrillar meshwork and the stress fibres (for details see Tillman & Bereiter-Hahn in preparation). Similar observations can be made, when the energy supply in endothelial cells (XTH-2-cells; [22]) is prevented by inhibition of respiration and lactic acid production. This condition is characterized by a lowered ATP content and a loss in tension of the actomyosin system (unpublished results). Block of energy metabolism causes an increase in cell volume, the decrease in surface reflectivity for ultrasound is less obvious.

These observations strongly support the suggestion of an intracellular hydrostatic pressure.

3. CELL SHAPE AND LOCOMOTION

3.1. General considerations

Three phenomena are inevitably related to shape of cells in tissue:

a) The presence of cytoskeletal elements

b) Adherence of cells and anchorage of fibrils to sites of adhesion

c) An intracellular hydrostatic pressure

The structural elements, which are important for shaping a cell and which drive locomotion, can all withstand tension and exert forces (actin fibres, microtubules, intermediate filaments). This tension, however, does not develop without the ends of the fibrils being fixed as is provided e.g. by focal contacts, desmosomes, intermediate junctions, and other sites of the cell membrane. This phenomenon becomes obvious in retraction of wound margins. Single or isolated cells maintain (or develop) their shape in relation to an adhesive substratum. A cortical fibrillar network associated with the cell membrane may become tensed without adhesion of the cell to a substratum. In this case the fibrils envelope the more central cytoplasm acting as an abutment, by its incompressibility a hydrostatic pressure is developed. The intracellular hydrostatic pressure is the third component related to cell shape. It results from the contractive force of the cortical actomyosin network interconnected with the plasma membrane. It forms a continuous cortical sheet. Therefore any contraction at any place of the meshwork adds to the state of the whole system. The contractile force is counteracted by the hydrostatic pressure exerted on the enclosed portion of cytoplasm.

Starting from these minimal organisational requirements a spherical cell would result. Any deviation from a spherical shape needs either a local weakening in the cortical network, which would result in bleb formation or a reinforcement by tensile elements like actin fibres or by stiff elements like microtubules. On the other hand the internal pressure provides counteraction for all contractions of fibrils traversing the cytoplasm and connecting different parts of the cortical network or peripheral fibrils with a perinuclear fibrillar reticulum [17]. Contraction of a fibrillar network in such a system of internal mechanical stabilisation is a structure generating process: The contraction proceeds as long as the resistance is less than the contracting force, then at equilibrium of the opposing forces the isotonic contraction becomes isometric, fibres develop from the isotropic network. In addition to this, inner resistance, adhesion to a substrate

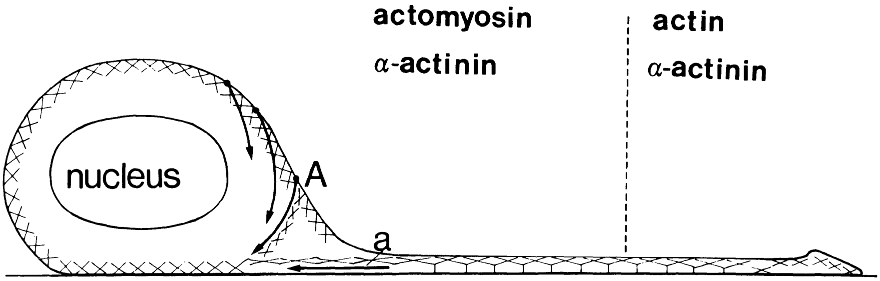

Figure 1. Cross section through a single, moving epithelial cell (epidermis cell) with semicircular shape (see inset, crossing line indicates section plane). Cross hatching symbolises actin meshwork, from which fibres A and a develop by a contraction against a resistance. Also depolymerisation of f-actin is supposed to occur in this zone. At the front end of the lamella oligomeric actin reassembles together with α-actinin. For further details see text.

provides an external abutment necessary for the development of fibres by contraction of an isotropic gel. Also formation of microvilli seems to depend on an internal hydrostatic pressure [3] .

The subtle interaction of contraction processes, assembly and disassembly of actin gels, controlled by ionic fluxes, that of Ca^+ in particular, and adhesion to a substrate is responsible for generation and maintenance of cell shape and locomotion.

3.2. Shape and locomotion of epithelial cells

Epidermis cells in culture are a well studied example to elucidate these interactions [4,20,24,25] : The locomotory form of single *Xenopus laevis* epidermis cells is roughly semicircular, a large lamella sharply distinct from the cell body is developed into the direction of movement. By fluorescence techniques actin can be demonstrated throughout the cell, with varying density, but not forming stress fibres. Myosin is found in the cell body and about in half of the lamella close to the cell body. Microtubules and tonofilaments do not appear to be related to locomotion [4] . From these fluorescence studies and EM-investigations the course of fibrils presented in Fig. 1 is deduced. Considering the existence of a hydrostatic pressure a hydraulic pressure hypothesis of locomotion is developed. Motive force is generated by a small pressure difference between the cell body and the edge of the lamella. The cortical actomyosin meshwork and the fibrils in the cell body-lamella-transition regions produce a hydrostatic pressure on the whole system. The lamella is kept flat by actin filaments interconnecting the dorsal and ventral membrane, adhesion to the substrate provides the anchorage. Weakening of the dorso-ventral interconnections at the front edge gives rise to a local pressure release by swelling and extension of the margin. The swellings have been named "microcolliculi" ("small hills"), they are supposed to be a functional equivalent of ruffles in fibroblasts [4] . Extension of the lamella at the front edge is compensated by a shortening at the cell body-lamella-transition region keeping lamella size approximately constant. This "shortening" is thought to result from a contraction of fibrils connecting cell body and lamella ("a" in Fig. 1). Contraction is supposed to be followed by disassembly of f-actin to oligomeric actin.

4. CRITICAL TESTING OF THE HYPOTHESIS

Potent tests for each hypothesis on cell locomotion are the questions whether the processes, which are thought to be involved, can be controlled by well known events and whether continuity of locomotion and self organization of the structural elements are explained. At least three processes have to be controlled:

i. Contractions. They are supposed to take place in the cell body-lamella-transition region, and probably in the whole cortical cytoplasm of the cell body.

ii. Disassembly of f-actin in the cell body.

iii. Sol-gel transformations at the leading edge.

Contractions serve two different functions, force generation for building up a hydrostatic pressure (arrow A in Fig. 1) and pulling the cell body into the lamella (arrow a in Fig. 1). Both functions are located at the same site in the cell, therefore they can be controlled by the same process, i.e. by calcium fluxes [25] . Whether other parts of cortical cytoplasm participate in contraction is still an open question: the presence of myosin is in favour of this assumption. In any case the cortex must be of sufficient strength to keep the internal pressure, otherwise bleb formation occurs. Calcium induced disassembly of f-actin has been demonstrated by Stossel and his group (for review see e.g. [23]). At the front edge of the lamella reorganization of an actin gel with the participation of α-actinin is supposed to take place. This process requires a low calcium concentration; calcium concentrations sufficient to trigger contractions induce solation [23]. The existence of a calcium gradient is well established in amoeba [30], different reactions in cell body and lamella to varying calcium concentrations are found in Xenopus epidermis cells (Mittal and Bereiter-Hahn, in prep.). Weakening at the front edge may result either from external stimuli mediated by the cell membrane or by random local solation of the thixotropic gel due to hydrostatic pressure.

Lamella formation and disintegration by pulling the cell body into the lamella have been describe above. This allows a continuous movement. Formation of fibres (A an a in Fig. 1) remains to be explained. Both are supposed to be pulled out from a fibrillar meshwork located either in the cortex of the cell body or in the lamella. Myosin is found only in the cell body and the proximal part of the lamella. This distribution is not yet understood, probably myosin forms relative large aggregates while streaming towards the leading edge, therefore being trapped within the actin network of the lamella.

5. COMPARISON OF EPIDERMIC CELL AND FIBROBLAST LOCOMOTION

Shape and locomotion of epidermis cells is typical for many epithelial cells in culture and corresponds very well to the behaviour of these cells during wound closure [21]. Their locomotion differs from that of fibroblasts in velocity and continuity. The main structural differences are the presence of stress fibres and focal contacts in fibroblasts and a more elongated shape. In fibroblasts the lamella is not as clearly distinct from the cell body as in epithelial cells. The question arises whether the same basic principles can be used to explain structure and behaviour of both cell types. Contraction of the cortical actomyosin-gel can be assumed to generate a hydrostatic pressure also in fibroblasts. Stress fibres reinforce the cell in lateral direction, therefore outflow of cytoplasm is directed to the long axis of the cell [27]. A short distance behind the advancing edge focal contacts form, and in second stress fibres appear [13]. They can develop by contraction of an isotropic actomyosin network traversing the cytoplasm. Due to fixation at the focal contact the fibre is pulled out of the gel by contraction of the gel. This type of development also explains the connections between stress fibres and the reticular gel structure (beautiful pictures of these structure are given e.g. by Heuser and Kirschner [11]). Contraction of reticular actomyosin and stress fibres exert the force to shorten an elongated fibroblast. This shortening is counteracted by the numerous focal contacts. When their adhesive power is overcome, the trailing end can be pulled towards the lamella (for illustration see for instance Dunn [8]). This contraction is followed by a burst of lamella activity and by transient increase in locomotion speed. Those events, however, take place after some seconds of delay following cell retraction as was thoroughly studied by Dunn [8].

The occurrence of the delay time is the main argument of this author against the idea of a hydraulic pressure gradient driving locomotion as was first proposed by Harris [10] for fibroblasts. This argument does not take into account that in pressure generation the whole cell is involved. Retraction of the trailing end into the cell body is an isotonic contraction of the retracting cytoplasm and first causes an increase in width of the cell body with a concomitant rearrangement of the contractile system. Only the more or less isometric contraction following the rearrangement phase can be expected to produce pressure.

Therefore locomotion of fibroblasts can be explained by the same mechanisms as proposed for epithelial cells. The much slower speed of locomotion and its discontinuity are a consequence of higher adhesion to the substrate. Also in epidermis cells fibres develop in the lamella, when the cell body adheres to other cells, being prevented from following the lamella.

6. CONCLUSION

Locomotion is a consequence of local instability of cell shape, therefore shape and locomotion are mutually interrelated. The considerations presented above favour a generalized model of cell locomotion, based on the analysis of shape of migrating cells. The model can be adapted to different types of cytoskeleton organization. Force generation by the cortical actomyosin meshwork and determination of direction by a local weakening of cytoplasm have been discussed by several authors [for instance 1,2,7,23, 26,27], the existence of a hydrostatic pressure, however, has not been considered in full consequence. Further planning of experiments regarding the control of locomotion is intimately related to the basic idea on locomotion, i.e. whether motive force is supposed to be generated in the lamella or in the cell body.

ACKNOWLEDGEMENTS

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ON THE RECONSTRUCTION OF PHYLOGENETIC TRANSFORMATIONS. THE ORIGIN OF THE ARTHROPODS.

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ABSTRACT

The conditions are outlined under which the body construction of annelids could have been transformed into that of arthropods. As an adaptation to a vagile life and an uptake of food by filtering particles from the sediment, the body was more and more flattened. Thus lateral protrusions, the subsequent pleurotergites, developed, and the parapodia were shifted to a more ventral position and could differentiate into the branched limbs typical for arthropods. This is the condition under which parts of the body wall were kept immobile, so that they could become sclerotized in the form of rigid plates.

1. INTRODUCTION

Evolution is the process of gradually changing the construction of organisms. The historical order of the transformations must be reconstructed theoretically on the basis of knowledge of existing organisms and fossils. The questions how and by what a certain change took place can only be answered in that the possible boundary conditions for a change are outlined. Thus the questions cannot be answered definitely; the reconstruction always has the form of a most likely theory. The procedure of reconstruction, as it was developed and has been used in our working team, shall be presented here by the example of the change of the annelid worm construction into that of the arthropods.

2. THE METHODOLOGICAL PROCEDURE

1) Theoretical background of our reconstruction procedure is a revised form of the evolutionary theory, as outlined by Gutmann and Bonik [4]. The organism is seen as an energy converting apparatus. Thus "selection tests not only the adaptation to a special environment, but also the biological apparatus" [7]. Variants with a better, more economic balance

of energy input and output of descendants must succeed in the long sequence of generations.

2) For reconstructing the phylogenetic transformations (see [6]) the initial conditions can be outlined, under which a biological apparatus could have been gradually changed. These conditions are sketched for the organismic construction and hence are based on the laws of physics and chemistry.

3) The starting point is a certain animal construction; it establishes the architectonic base. This is altered in a way that efficiency increases. Hence, the resulting construction is determined by both the architectural preconditions and the special alterations, required by the environment and the construction.

4) Increase of efficiency is always comparative. Any increase of efficiency in what part of an organism for ever counts (and pays) for the whole.

5) Quantitative calculations in models are possible, as shown by Bonik [1], for the balance of longitudinal and circular muscles in the hydrostatic wormlike body construction. In many cases, however, evidence is so striking that such calculations may be omitted.

6) Constructional alterations are irreversible, since they change the architectonic base. From the new base a new evolutionary transformation may start, but it must result in a new animal body construction, because it must result in a new animal body construction, because it starts from the new base (not from the ancestral one). A main constructional alteration is always a way of no return.

The subject of analysis in this paper is the transformation of the annelid worm construction into that of the arthropod. This transformation, being called "arthropodization", is widely undoubted because the morphological similarities of the two groups are very obvious, and intuitively the morphocline was polarized as a sequence starting from annelids and leading to the arthropods. The first attempt to reach an explanation of the "how and why", however, were made by Lauterbach [5] and, in a more precise and detailed way, by Bonik, Grasshoff and Gutmann [2] and Grasshoff [3]. The gap to be bridged between the two animal groups is rather wide.

3. THE BASIC CONSTRUCTION: THE ANNELID

The annelid construction is a soft-bodied hydrostatic system. All parts are flexible. Muscles and connective tissues are arranged as longitudinal and circular muscles in the body wall and as transversal, dorsoventral and oblique muscles crossing the body cavity. Often the muscles are attached to dissepiments, which generate compartments. The body is constructed segmentally. Each segment bears lateral protrusions, the parapodia, partly stiffened by setae. They act in locomotion as paddles or for various different motoric purposes. The fluid of the body cavity, the coelom, as well as the contents of the intestinal tract act together as the hydrostatic filling of the system.

4. THE DERIVED CONSTRUCTION: THE ARTHROPOD

The arthropod construction is basically also a hydrostatic system. However, parts of the soft wall are sclerotized forming more or less rigid plates or tube-like skeletal pieces in the rather slender appendages. These plates and tubes may come so close together that they are linked in joints, but the connections between the rigid parts are always constituted by the soft body wall. For all arthropods in all stages the combination of a soft body hydrostatic system and a skeletal muscle system is typical.

5. SPECIFYING THE GENERAL QUESTION

We assume the above-mentioned preliminary hypothesis, based on morphological evidence of the similarities in segmentation, nervous system *etc.*, that the arthropod construction has to be derived from the annelid-like precursor construction. In consequence, our question is: under what conditions was a sclerotization of the body wall possible.

We may not expect any aid by morphological evidence of fossil or existing animals. Fossils of early arthropods are either fragmentary or fully developed arthropods in the complete form of trilobites or the Burgess shale species. In any way, they are not showing transitional stages. The onychophorans were oftenly claimed as "missing links", but they are surely not (we'll focus on this problem shortly in the end of this analysis).

In general, the precondition for sclerotization in a soft body system consists of the parts that are kept immobile by the stabilizing interaction of muscles and fluid pressure, *i.e.*, in an active way. From the very beginning of the occurrence of the skeletal structures a positive selective value must be present. It is provided by the saving of matter and energy to maintain a certain body shape. With the onset of skeletal development this is effected in a more economical way than by the bracing influence of expensive muscle action.

6. CONDITIONS FOR SCLEROTIZATION IN THE WORM CONSTRUCTION

Where can be expected that body parts are kept immobile although under stress in the annelid worm construction? In existing polychaetes we do not find such conditions. All those species are specialized in a certain way for swimming, tube-dwelling, creeping in the sediment, *etc.*, using mostly the mobility of the whole body. Thereby no parts are excluded from deformation (Fig. 1). The worm representing the arthropod ancestor cannot have been a specialized swimming or tube-dwelling animal. This worm construction must have been very versatile and able to perform a variety of behavioural actions, as lying and grubbing in the upper layers of the sediment, often leaving it, and moving to new places in search for food. While lying in the sediment, a tube was formed under the ventral side of the body; the parapodia grubbed and filtered particles and effected (because they were acting within a tube) a water flow running to the mouth. Such actions were observed in living polychaetes, in various modifications. However, the species having such modes of nutrition are more specialized than those we have to assume for the arthropod ancestor.

As an adaptation to this way of life and these actions, an important alteration could have taken place: the body became more and more flattened. The flattening took place in the dorsal part of the body, supporting the "roof" of the sediment tube. Here the pleurotergites of the (subsequent) arthropodes originated (Fig. 2, 3). Thus the tube was enlarged so that the parapodia gained more freedom of movement for the power stroke effecting the water flow and for more differentiated movements of grubbing and filtering. The position of the parapodia was not altered basically, but they were shifted relatively from a more lateral to a more ventral position. Their interaction in the ventral middle line was not only guaranteed, but could be improved, in the course of all following differentiations, transforming the parapodia into legs.

In the beginning, these alterations could have been effected by muscle action, later they became the stabile body shape. Noteworthy in the arrangement of connective tissues and muscles are the transversal connective

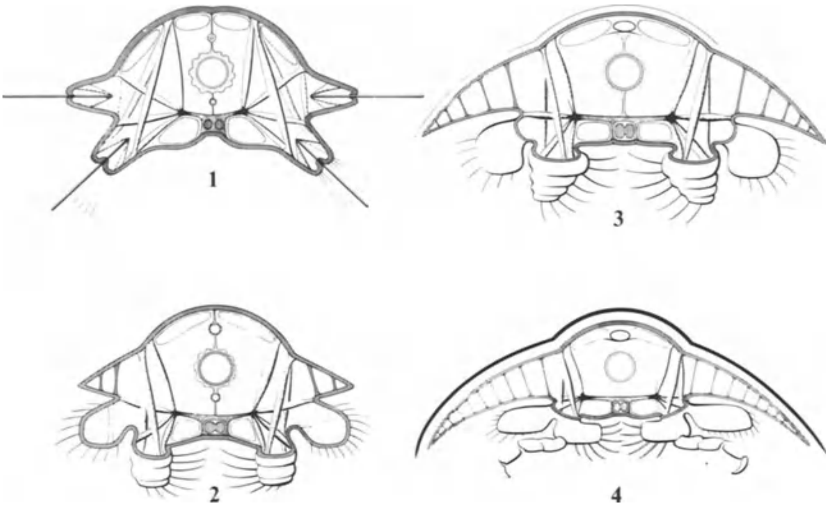

Figure 1-4. The transformation series from the annelid worm construction to that of the arthropod. Mechanically most important parts in schematic transverse sections through body segment.
Figure 1. Generalized annelid construction. Muscles outlined as thin bands for better clarity. Transversal connective tissue bridge above nervous system.
Figure 2. Beginning of body flattening and of the lateral extrusions subsequently developing to pleurotergites. Shifting of parapodia into a more ventral position.
Figure 3. Flattening of body progresses. Thin upper line indicates that the longitudinal musculature (dotted fields) separates from the body wall in the middle of the segments (compare Fig. 5).
Figure 4. Differentiation of limbs; medial part transporting food particles along the ventral groove, lower part grubbing and scratching, also used for locomotion; upper part (shown in outlines only) with various functions, as raking, filtering, respiration, *etc*. Development of sclerite in the dorsal body wall indicated by heavy black line.

tissue belt above the parapodia, the dorsoventral fibers and muscles in the flattened lateral parts, and the muscles running from the dorsal body wall into the extremities. This arrangement was maintained basically up to the arthropods (Fig. 4, 5).

Following this development, parts of the parapodia may have been differentiated for different functional roles of scraping, raking, filtering, transporting food particles to the mouth, and for respiration, as well. Since parapodia are usually split in at least two lobes, the architectonical precondition was established for the development of the branched limb.

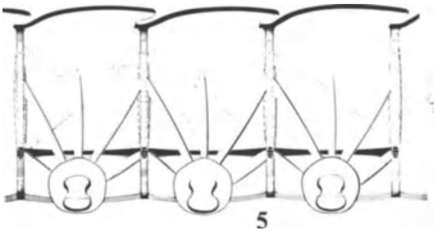

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Figure 5. Schematic sagittal section through segments of level 4. Longitudinal musculature (dotted strips) inserts at the connective tissues originating from the dissepiments, which have already disappeared in this evolutionary stage. Locomotion is effected mainly by the legs (insertions schematically, in the middle of the segments). The bulged-out regions of the segments (dorsal) are held relatively immobile, consequently sclerotization begins here.
Figure 6. Schematic dorsal views of the transitional stages from the worm to the arthropod. Design: Hermann Schäfer.

It is basically composed of a slender, ventral branch for grubbing and scraping, a dorsal ramus for raking and filtering, whereas the medial edge of the basal part is free for transporting particles along the ventral groove.

As a result of the differentiation of the parapodia and the flattening of the body, the construction could not only function in the sediment, but also on the surface. This was caused by two factors, (1) the tube, necessary for making a water flow, was now established by the animal body itself, and (2) the appendages could be used for effective locomotion. Thus these pre-arthropods were enabled to live and to obtain food also on harder sediment surfaces and on rocks by scraping the surfaces. The transition to locomotion on the surface was an important step, since it was no longer effected by deformation of the whole body, but by parapodia, which can be called limbs from this stage of transformation on.

In this situation the body trunk is held immobile by muscle action and fluid pressure so that advantage is taken of moving the limbs only for locomotion. For those animals living on the rather hard surface of the sediment or on rocks this is the condition for building up rigid parts in the body wall.

The process of sclerotization probably begins in the dorsal part of the middle of the segments, and in the grasping part of the limbs. Sclerotization may extend more and more and stops only, where the narrow zones between the rigid plates and tubes are indispensable for the body movements, as seen in living arthropods.

7. RESULT: THE ARTHROPOD CONSTRUCTION

The final stage of these transformations is the typical primitive arthropod as we find it in the early fossils as trilobites and similar forms. New in this animal construction, as compared to the ancestors, besides the rigid skeletal parts, is that bending of the body became restricted to the dorsoventral direction. In the old worm construction, bending by the almost unlimited deformability of the body could occur in all directions, and transversal undulations were preferably made for swimming and for the support of ambulatory movements of the appendages (Fig.6).

Some important features of the old worm construction remained: the way of life and of gaining food by scaping raking and filtering, the transport of food along the ventral groove, and the large extended upper lip under which the foremost limbs are stuffing the concentrated food particles into the mouth. Moreover, the arthropod body is, like the worm ancestor, basically a soft body hydrostatic system, which can never be abandoned.

The main lines of further radiation may be roughly characterized as (1) increase of efficiency in the level outlined above of grubbing and filtering the surface layers of the sediment (trilobites), (2) as the development of filter feeding in the free water (crustaceans), and (3) as transition to predacious habits (chelicerates).

From these viewpoints it becomes clear, why the onychophorans cannot be regarded as transitional stages between the worm and the arthropod construction. Their body is a fully hydrostatic acting system. Bending in all directions, penetrating narrow crevices, stiffening the body trunk for a short time only, when they use the legs for walking, they are fully adapted to their terrestrial environment, under leaves, stones or logs. Their body shows no part, in which a sclerotization could be estimated to be advantageous. The onychophorans are standing in a dead ending evolutionary line, which left the arthropod line very early, or developed independently of it from the annelid worm construction.

8. A WAY OF NO RETURN?

Perhaps nobody has doubt in the (theoretical) statement that the annelid worm construction represents the primitive and the arthropod the advanced phylogenetic level. But what is the crucial point that allows to preclude the opposite evolutionary direction?

If the transformation (from the worm to the arthropod) was an increase of efficiency with respect to the actions of the body construction, then the opposite direction would be a decrease of efficiency. Such transformations are excluded by the evolutionary theory. This does not rule out that, under certain circumstances, the arthropod construction can be rehydraulized by reduction of rigid skeletal parts. The starting point of such a transformation, however, is an arthropod and thus the architectonical conditions of its construction would have to be gradually altered. Thus the resulting construction would be a derived arthropod, and never more an annelid worm. Too many features are already changed, too much of the old architectural base is already lost, *e.g.*, the material for the (re-)organization of a closed blood circle or a coelothelic lining is no more available, as it had once been in the ancestral construction. In this sense the change of the body construction is a way of no return.

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[51]

MECHANICAL CONSTRAINTS CANALIZING THE EVOLUTIONARY TRANSFORMATION OF TETRAPOD LIMBS.

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ABSTRACT

A reconstruction of the anagenetic transformations from fins to tetrapod limbs is represented considering the self-evident mechanical constraints which must have limited the construction and thus the function and the transformation.

1. INTRODUCTION

According to the maxims given by Peters & Gutman [8] , Peters [7] , Gutmann & Peters [3] the reconstruction of anagenetic evolutionary processes cannot be achieved by merely comparing the arrangement of elements of organismic structures. On the contrary, it is necessary to understand the constructional and functional properties of the structures under investigation. The reconstruction has to be a model of the transformation stressing the continuity of adaptive advantages for the successive constructions. Thus this paper will not present new or additional arguments concerning the genealogical relationship between tetrapods and a certain group of fishes, although it is assumed of course that some fishes must have been the ancestors of tetrapods.

The mere fact that tetrapods are *tetra*pods, says that they have four legs, is corroborating this assumption quite strongly. As is demonstrated by insects, spiders, crabs, millipeds, lions, kangaroos and men, terrestrial locomotion can be realized with very different numbers of limbs. Terrestrial conditions as such apparently are not acting as sufficient selection forces in favour of only one specific number of legs in walking organisms.

On the contrary there are obviously constraints limiting the number of paired fins in fishes, two pairs being the optimum system controlling the equilibrium [2,4,5]. Fishes which became ancestors of tetrapods began to walk with these two pairs of fins.

This is the starting point of the transformation. The final one is the construction of the typical tetrapod limb with stylopodium (one bone), zeugopodium (two bones) and autopodium (many bones). We are interested in the transitions between these two points, and we are interested in the question whether or not the pattern of elements in a tetrapod limb was determined exclusively by a homologous patterns in the ancestor. In other words we shall have to reconstruct the anagenetic transformations which must have happened on the evolutionary pathway from one point to the other, bearing in mind that we are not dealing with a simple transition of form, but with a continuous series of functioning mechanical machineries [9].

2. THE INVENTION OF WALKING

It seems very improbable that tetrapod limbs should have evolved from the flexible blade of fins if fishes did not aquire the ability to walk on their fins before entering terrestrial environments. Walking means not only to make steps but also to lift the body from the ground. I agree with Bonik [1] who pointed out that fishes gliding on their ventral surface by undulating movements and using their fins only to provide lateral stability never could give rise to tetrapods. Such organisms would have been able to improve their terrestrial locomotion only by better gliding. Since the transition from a paddling blade to a supporting strut could not happen at once, there is no doubt that the first efforts to stand and to walk on land would have been much less efficient than the well established technique of gliding.

Thus we have to assume that the ancestors of tetrapods became "walkers" already during their aquatic life. Under aquatic conditions it is much easier for a fin to act (at first sometimes, then for longer and longer periods) as a supporting limb since a submerged body, according to Archimedes' law, is much lighter and thus can be supported with less effort than under terrestrial conditions. In this respect it seems even possible that most if not all of the transition from a fin to a leg happened in aquatic or semi-aquatic environments.

It is noteworthy that fishes "walking" in different ways are well known at present too, *e.g.* many species of *Triglidae*, *Gastromyzonidae*, *Antennariidae*, *Anabantidae*, *Clinidae* and *Periophthalmidae*. One gets the impression that fishes would invade terrestrial habitats again and again were these habitats not occupied already by tetrapods.

3. THE CLUMSINESS OF FINS AS WALKING EXTREMITIES

Fins usually are distally broadened blades with increasing flexibility toward their distal margin. Thus standing or walking fishes have to extend their fins laterally and to touch the ground with the broadened distal parts. They cannot bring the fins in a vertical parasagittal position and stand on "tiptoe". But even if they were able to stand in this way they would be unable to walk, because as Gray [2:82] stated correctly: "... if the animal is to lift its fin off the ground when the centre of pressure of its bearing surface is vertically under the joint which unites the fin to the body there must be at least one moveable joint between that of articulation to the body and ... the plantar surface."

Of course, walking with laterally extended fins is not a light-footed gait either. Above all two difficulties deserve more detailed consideration:

a) Although a fin usually is more or less flexible it cannot be folded, and because of its flexibility bending under the weight of the body cannot be prevented. In consequence the distance between the bearing surface and the base of the burdened fin cannot be changed actively. This means *e.g.* that the animal walking on rough ground will be forced to make many unintended movements which would be induced by the unevenness of the ground and not be compensated by the relatively rigid fins.

b) The virtually unchangeable distance between the bearing surface and the basal joint of the fin brings about also a laterally undulating movement of the body. In the course of each step the proximal base of the supporting fin moves compulsorily on the segment of a circle around the bearing surface, while the latter must rotate on the ground in the opposite direction (Fig.1). This gliding component of the bearing surface's movement reduces the propulsive effect of the power expenditure as well as the save foothold of the animal. It makes no difference for our considerations if we assume that the undulating movement of the body was inherited already from the swimming ancestors since it is anyhow a mechanical constraint. When the animals started walking, they had to maintain this movement (and to adapt it to walking) or to introduce it *de novo*. In any

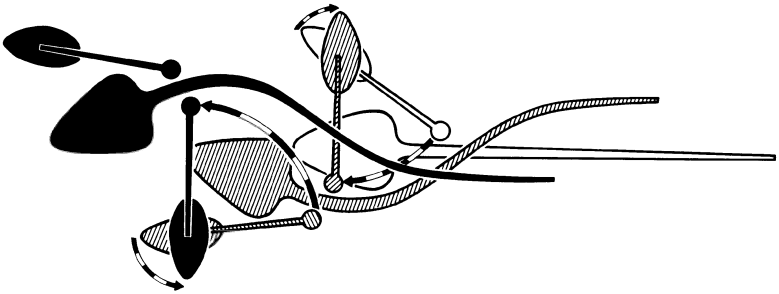

Figure 1. Walking with laterally extended jointless limbs. During propulsion the body is forced to make undulating movements while the bearing surface is rotating in the opposite direction.

case the vertebral column of the ancestor of tetrapods must have been able to bend laterally.

4. MINIMIZING THE CLUMSINESS

In order to overcome the difficulties described in 3.a and 3.b at least four improvements had to evolve:

1) Muscular and skeletal elements had to invade the fin. By means of these elements the flexibility of the fin could be controlled to a certain degree by active forces.

2) The controlled flexibility of the fin had to be transformed finally into the most parsimonious and effective system, which is made by two favoured bending zones (joints), one between the bearing surface and the handle, and the other one within the handle, thus giving rise to a limb with three main partitions. By means of this construction the disadvantages mentioned in 3.a could be remedied in the most economical way (Fig.2).

3) The sliding rotation of the bearing surface (autopodium) against the ground during propulsion had to be replaced by rotation within the limb. With the material given (endoskeleton of bones or cartilage, muscles, ligaments), only two solutions of this technical problem seem to be practicable. In both cases the most proximal partition of the limb (stylopodium) should consist of one bone since a limb used as a walking limb should be connected with the body by a multiaxial joint, which is realized in the best way by a single element rolling in the socket. In the middle

Figure 2. The flexible blades of fins cannot be folded (left); their flexibility can be controlled actively by adding muscular and skeletal elements (middle); the optimal control of "folding" and "unfolding" movements can be achieved by establishing two new joints between the bearing surface and the proximal base of the limb (right).

partition of the limb (zeugopodium) two constructions are possible: a) one bone with multiaxial joints; b) two parallel bones, which during the propulsive phase would change the relative position of their distal ends only very slightly, while their proximal ends would turn around each other in coordination with a rotating movement of the stylopodium, this results in an X-shaped crossed position of the two bones. It seems unnecessary to stress, that this construction cannot be improved by a zeugopodium consisting of more than two bones.

There is no doubt that from the technical point of view the second solution is the better one. At first glance a multiaxial joint might seem to be the best construction to fulfil twisting movements, but it is a very expensive one, too, because all unintended movements have to be suppressed by muscles. The greater the mobility of a joint the more power is needed to stabilize this joint. A ball-and-socket joint between stylopodium and zeugopodium and/or between zeugopodium and autopodium would require more muscles and a greater capability of coordination than the second solution which is combining the advantages of twistable elements with comparatively stable articulations.

In the latter case the twisting component of movement in the zeugopodium can be controlled by muscles acting on the stylopodium. These muscles are attached to the girdles and to the axial skeleton which contrary to the bones of the limbs offer extensive surfaces for a strong muscular system.

Tetrapods realized the second alternative of construction as is well known. The movements of primitive tetrapods were thoroughly described and figured by Schaeffer [10], therefore no further explanation seems necessary.

(Schaeffer's Fig. 3 was cited several times, *e.g.* Peters & Gutmann, [9, Fig. 4]; Starck, [11, Fig. 421]. It was overlooked that in Schaeffer's Fig. 3A the forelimb was erroneously drawn showing the radius crossing the ulna from behind.)

4) After the stylopodium and the zeugopodium were capable of performing rotating movements, the autopodium could improve its newly gained firm foothold by splitting the bearing base into several marginal lobes, each with a multisegmented skeleton. By these lobes (fingers and toes) the autopodium could take a better grip upon the ground. There seems to exist no plausible explanation for the fact, that just five lobes evolved.

In the zone where the autopodium is connected with the zeugopodium it has to compensate the pressing and pulling forces originating from the zeugopodium. Therefore this zone should be tight but not stiff. Many small bones embedded in cartilage and connective tissue seem to be an appropriate arrangement for this purpose. It is also clear that in this zone a variation of arrangement is more tolerable and necessary than in any other part of the limb.

In the course of the four improvements mentioned above the fin will be transformed into the construction actually found in primitive tetrapods with the canonical pattern of elements: *humerus* (*femur*), *ulna* and *radius* (*fibula* and *tibia*), *carpalia* (*tarsalia*), *metacarpalia* (*metatarsalia*), *phalanges digitorum*. It should be noted that the sequence of improvements is not arbitrary, but consists of a necessary succession of functioning constructions.

5. TESTING THE MODEL

If our model sketching the transition from a fin to a tetrapod limb meets reality the following two predictions are testable:

1) Whenever the limb does not rotate axially the "canonical" pattern of elements of the limbs should tend to be simplified.

This is indeed the case, as can be seen in many mammals (esp. ungulates), many archosaurian reptiles and in the pelvic limbs of birds. The limbs of these animals are no longer extended laterally, but in the same vertical longitudinal plane as their basal joints. Moving in a parasagittal plane they are not forced to make twisting movements. Thus the zeugopodium and the autopodium can be optimized by reducing and fusing elements which are in this configuration without function. We do not find such modifications in animals with laterally extended limbs.

2) Since in our model mechanical constraints are canalizing the transformation, the arrangement of bones in primitive tetrapod limbs should be identical even if the limbs derived from fins with differing arrangements of bones.

Although arguments suggesting a diphyletic descent of tetrapods were put forward repeatedly we shall not consider this case here. Even if we are assuming monophyly of tetrapods the prediction is confirmed.

The patterns of the pectoral and the pelvic limbs of tetrapods are virtually identical. Yet in all recent and fossil fishes there is a clear difference between the pectoral and the pelvic fin. "This must be taken to mean that the fore limb and the hind limb in each tetrapod have arisen independently of each other from two different patterns of arrangement. In other words the pentadactyl limb has arisen at least twice." [6:132].

6. CONCLUSION

The "Bauplan" of the tetrapod limb is not a randomly arranged configuration of elements, but a construction which has to be regarded as the result of a transformation limited by mechanical constraints. It cannot be explained by merely comparing its arrangement of elements with the allegedly similar arrangement in the fins of *Eusthenopteron*, *Sauripterus* or other fishes. Of course, the starting point of the change must have been fins whose construction permitted a gradual transformation into a tetrapod limb. This necessary condition does not preclude however a variety of primary constructions within certain limits. In other words the "Bauplan" of tetrapod limbs although being the apomorphic condition as compared with a fin is not necessarily a synapomorphy of all tetrapods. Thus the "Bauplan" of tetrapod limbs *per se* does neither indicate monophyly nor polyphyly of tetrapods. My model is consistent with the current theoretical assumption that *Osteolepiformes* are the ancestors of tetrapods, but this does not mean that other theories (*e.g.* deriving tetrapods from porolepiforms or dipnoans) are therewith falsified.

With regard to the main heading of this workshop the model can be considered as a case study exemplifying the methodological maxims formulated by Peters & Gutmann [8], Peters [7], Gutmann & Peters [3] for the reconstruction of evolutionary processes.

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THE LEGS OF OSTRICHES (*STRUTHIO*) AND MOAS (*PACHYORNIS*)

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ABSTRACT

Ostriches were filmed running at maximum speed, and forces on the feet were calculated. Measurements were made of the principal structures in the legs of an ostrich. Hence peak stresses in muscles, tendons and bones were calculated. They lay within the range of stresses calculated for strenuous activities of other vertebrates. The ostrich makes substantial savings of energy in running, by elastic storage in stretched tendons.

Pachyornis was a flightless bird, much heavier than ostriches and with massively thick leg bones. These bones are shorter than predicted for its estimated body mass, by extrapolation from allometric equations for flying birds. An attempt is made to calculate the stresses that acted in the leg bones in running, for all possible patterns of leg movement. The stresses were probably rather low, unless *Pachyornis* was capable of running fast. It is argued that the optimum factor of safety for moa leg bones may have been exceptionally high, as a consequence of the absence of predators.

1. THE QUESTIONS

The investigations described in this paper posed two main questions.

(i) What stresses act in the bones, tendons and muscles of the legs of an ostrich (*Struthio camelus*) when it runs fast [9] ? This question asked for facts, not explanations, but it was hoped that the answers would help us to understand the structure of ostriches.

(ii) Why were the leg bones of moas such as *Pachyornis* so thick, in comparison with ostriches [2,3] ? This question seeks an explanation. Why did selection in moas favour leg bones so different from those of ostriches?

2. OSTRICHES

Fast running was chosen as the normal activity likely to impose the largest loads on the legs. Larger forces may occur in falls and other accidents, but are not predictable. It was decided to study wild ostriches

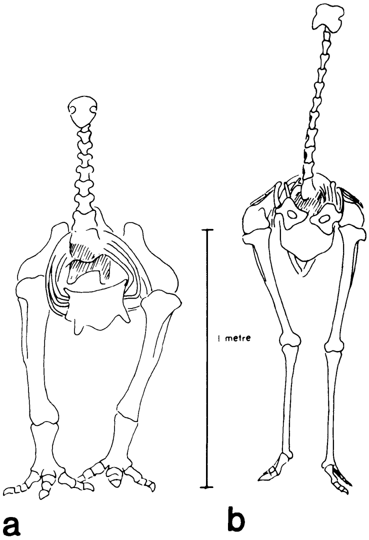

Figure 1. Skeleton of (a) a moa, *Pachyornis elephantopus* and (b) an ostrich, *Struthio camelus*. From Alexander [2] by permission of the Zoological Society of London.

in their natural habitat, because captive animals are likely to have suffered from lack of exercise. Consequently, forces on the legs had to be estimated from films: if captive animals had been used, the forces might have been recorded by means of a force platform.

The faster an animal runs, the lower in general is the duty factor (the fraction of the duration of the stride for which the feet are on the ground) and the larger are the forces on the feet. Ostriches were chased as fast as possible with a vehicle, over level grassland [6]. Films showed a minimum duty factor of 0.29. Force platform records of other species (including *Rhea*, [9]), running less fast, show that peak forces can be estimated fairly accurately from duty factors: a duty factor of 0.29 indicates a peak force of 2.7 times body weight. They also show that the peak force acts at the mid-point of the period of contact of the foot with the ground,

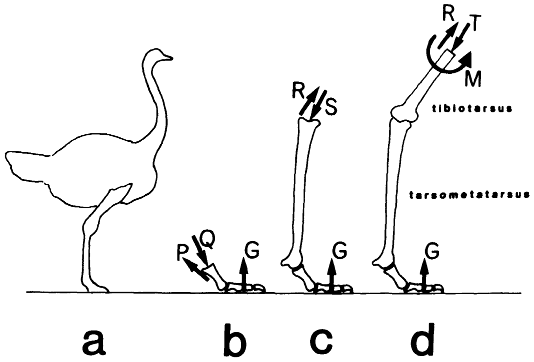

Figure 2. (a) An ostrich traced from a film of fast running. (b), (c), (d) Free body diagrams of parts of the leg. The ground force *G* is estimated to be 2.7 times body weight. The forces *Q* and *S* are reactions at joints. The other forces, and the moment *M*, are explained in the text.

and is approximately vertical. It was therefore assumed that a vertical force of 2.7 times body weight acted on the foot of the ostrich, at the instant illustrated in Fig. 2a. (Small deviations from the vertical would have affected the calculations only a little.) It was assumed that this force acted halfway along the part of the principal toe that was on the ground. (Ostriches have only two toes, one much larger than the other.)

These assumptions made it possible to calculate various forces in the leg, at the instant shown in Fig. 2a. The principle of the calculations is illustrated by the free-body diagrams in Figs. 2b,c,d. (Alexander [4] gives an explanation of free-body diagrams. The weights of leg segments, and the inertia forces and inertial torques on them, were ignored because they were small compared to other forces and moments.) Consideration of Figs. 2b,c makes it possible to calculate the forces *P* and *R*, in the digital flexor muscles and the extensor muscles of the ankle, respectively. Once *R* is known, consideration of Fig. 2d makes it possible to calculate the force *T* and the bending moment *M* acting across a section through the tibiotarsus.

The legs of a 42 kg ostrich were dissected. This was an apparently healthy bird, shot in the wild: a zoo specimen would not have been suitable because its muscles might have been reduced by lack of exercise. It was assumed that the dissected bird was geometrically similar to the one that was filmed. Thus dimensions taken from the dissection could be used with forces calculated from the film, to calculate stresses in bones, tendons and muscles. The stress in the digital flexor tendons was obtained by dividing the force *P* (Fig. 2b) by the cross-sectional area of the tendons. The methods used for calculating stresses in the (pennate) digital flexor muscles, and in the tibiotarsus, are explained by Alexander [4].

The following stresses were calculated for the instant shown in Fig. 2a. If the assumptions are correct they are the maximum stresses occurring in these particular structures, in a very fast running stride. The calculated stress in the digital flexor muscles was 0.24 MPa, and the stress in their tendons was 32 MPa. (This value has been corrected for an error in the original determination of cross-sectional area, explained by Alexander [1].) The calculated stresses in the tibiotarsus ranged from 70 MPa in the anterior face to -110 MPa in the posterior face.

The stress in the muscles is only a little less than the maximum of which vertebrate striated muscle seems capable, in isometric contraction. It is about equal to maximum stresses calculated for mammal leg muscles, in fast running and strong jumping [11]. The stress in the tendons seems to be about 40% of the tensile strength of tendons, and the extreme stresses in the tibiotarsus seem to be about 40% of the tensile and compressive yield stresses of bone. Thus the tendons and bone seem to have factors of safety of about 2.5, like many of the other tendons and bones for which data are available [1].

It seems well established that large mammals save energy when they run, by exploiting tendon elasticity [5]. When a foot is first set down it exerts a braking action, removing kinetic and gravitational potential energy from the body. Later in the step it exerts an accelerating action, replacing that energy. Without an elastic mechanism, the energy lost in the first stage would have to be dissipated as heat, and replaced in the second stage by work done by muscles. Instead, much of it is stored as elastic strain energy in stretched tendons, and returned in an elastic recoil. Thus the work required of the muscles is greatly reduced. Do ostriches save energy in the same way?

If ostrich tendon has the same Young's modulus as sheep tendon [12], the calculated stress of 32 MPa stretched the digital flexor tendons by 2%, or about 15mm in a 42kg ostrich. The calculated force *P* was 4500N, and the strain energy stored in the stretched tendon was about $\frac{1}{2}$(force)x (extension), or 34J. Alexander *et al.* [6] estimated that the stride length of the ostrich, in the film sequence that they analysed, was about 5m. The kinetic and potential energy lost and regained in each half stride can therefore be estimated as 70J, for a 42kg animal (equation 3 of Heglund *et al.* [10]). Thus a substantial fraction of the energy that would otherwise be required for fast running, is apparently saved by elastic storage in the digital flexor tendons.

This investigation showed that ostriches resemble cursorial mammals, in the maximum stresses normally imposed on the component tissues of their legs, and in the importance of tendon elasticity for running.

3. MOAS

This section is about *Pachyornis elephantopus*, one of the extinct moas. It is not the largest moa, but is the most impressively robust, and was heavier than any modern bird. Estimates of its body mass averaged 137kg: these were obtained from the volume of a model representing a plucked but otherwise intact bird, by scaling up to the dimensions of three different skeletons [2] . In contrast, the mass of a large male ostrich was only 81kg.

The aim, of the investigations that will be described, was to explain the striking difference of build between the moa and the ostrich (Fig. 1. Alexander [2,3]). It seemed appropriate to ask first, which of the two was out of line with birds generally. Is the moa more robust than would be expected for a bird of its mass, or is the ostrich more slender than would be expected?

Fig. 3 shows the lengths and diameters of the tibiotarsi of birds, from small passerines to the largest moas. The lines were obtained by model II regression of all the data for flying birds. (Model I regression lines would have gradients which were less by 0.01 in each case.) The graph shows that ostriches have tibiotarsus lengths approximately as predicted by extrapolation from flying birds. *Pachyornis*, however, had tibiotarsi only about 0.8 of the predicted lengths. The data for diameters show rather surprizingly that the ostrich has rather thick tibiotarsi for its body mass, and the moas have tibiotarsi of about the predicted diameters. Note however that the graph shows sagittal diameters, whereas Fig. 1 displays only transverse diameters. A graph for the tarsometatarsus (Fig. 4 of Alexander [2] shows that ostriches have tarsometatarsi a little longer than predicted for their body masses, and that *Pachyornis* have tarsometatarsi much shorter than predicted. The general conclusion from allometric

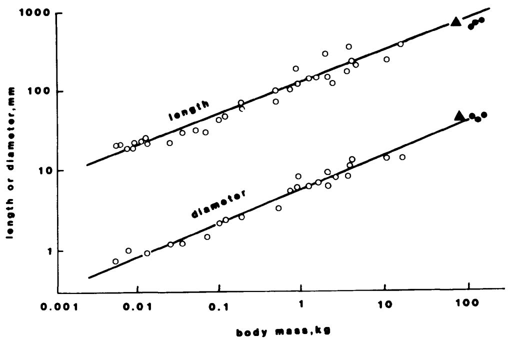

Figure 3. A graph on logarithmic coordinates showing the lengths and diameters of the tibiotarsi of birds, plotted against body mass. ● , *Pachyornis*; ▲ , *Struthio*; o , flying birds. The regression lines are based on the data for flying birds only. Modified from Alexander [2] .

comparisons is that *Pachyornis* leg bones are shorter than expected for their body masses, but have about the expected diameters. The allometric analysis also shows that there is nothing very extraordinary about the proportions of moa leg bones: data for some living birds deviate more from the regression lines, than do the data for moas.

Long bones are more at risk from bending moments, than from axial loads [3] . Strength in bending depends on the length of the bone as well as on its cross-section: a longer bone must be thicker, to withstand a given force. How did the relatively short leg bones of *Pachyornis* compare in strength with the longer leg bones of ostriches?

Alexander [3] used a quantity Z/mgx as an indicator of strength in bending. Here Z is the section modulus for a section through the shaft of the bone, at a distance x from the distal end, and mg is the weight of the body. Thus Z/mgx is the reciprocal of the maximum stress that would occur in the section, when the bone was loaded at its distal end by a force equal to body weight, acting at right angles to its long axis (see [4] , on the theory of bending). If different animals run in dynamically similar fashion and have homologous bones with equal values of Z/mgx, the stresses set up by bending moments in those bones will be equal (see [7], on dynamic similarity). Larger values of Z/mgx imply greater strength. Values of Z/mgx were calculated from bone dimensions, for *Pachyornis* and an ostrich. The values obtained were almost exactly equal in the case of the tibiotarsus, but the moa values were twice the ostrich values in the cases of

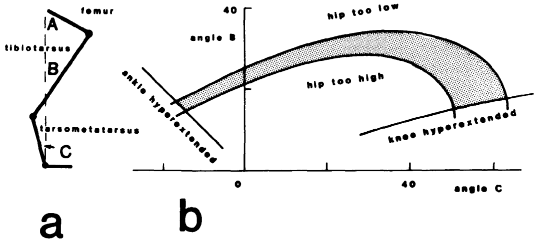

Figure 4. (a) A diagram of a moa leg, at the stage of the stride when the hip was over the metatarsophalangeal joints and the force on the foot was probably maximal. (b) A graph showing the range of possible combinations of angles in (a) (stippled). Modified from Alexander [3].

the femur and tarsometatarsus. Thus the femur and tarsometatarsus of the moa seem remarkably strong, in comparison with the ostrich, but the tibiotarsus does not.

Unfortunately for this line of argument, moas could not have run in dynamically similar fashion to ostriches, because the relative lengths of their leg segments were different. The ratio of lengths femur:tibiotarsus: tarsometatarsus is about 1:2:1 for *Pachyornis*, but about 1:2:2 for ostriches. Among modern birds, kiwis (*Apteryx*) and geese (*Anser*) have leg proportions fairly close to those of *Pachyornis*, but do not necessarily run like it.

Alexander [3] tried to avoid doubtful assumptions about moa leg movements by examining the whole range of possibilities. Fig. 4a represents a leg with proportions like those of *Pachyornis*, at the stage of the stride at which forces and bone stresses were probably largest. Notice that angles A,B,C can take a range of different values, for any given hip position. Fig. 4b shows the combinations of values that seem possible.

The few sets of moa footprints that have been found show short strides, indicating walking speeds. It nevertheless seems likely that moas could run. Modern birds and mammals generally walk at speeds u which make the Froude number $u2/gh$ less than 0.5, and run at higher speeds (see [7] : g is the acceleration of free fall and h is the height of the hip joint from the ground). Peak stresses were calculated for *Pachyornis* running slowly, at 3 m s^{-1} (Froude number 1.0). Separate calculations were made for several different leg positions, within the range of possibilities shown in Fig. 4b. These calculations indicated stresses up to about half the stresses that had been calculated, for ostriches running fast. Two possibilities have to be considered. First, *Pachyornis* may have been able to run faster. An increase to 10 m s^{-1} would have about doubled the stresses [3]. Secondly, *Pachyornis* leg bones may have had higher factors of safety than those of ostriches. In any case, the calculated stresses were not remarkably low, in comparison with published data for species other than ostriches.

Alexander [1] presented a theory of optimum factors of safety. Too weak a bone is likely to break but too strong a one is cumbersome. Let $P(S)$ be the probability that a bone of factor of safety S will fail in use. If it does fail, the animal incurs a cost F (which may be measured as loss of fitness, or in some other currency). Let $G(S)$ be the cost of growing a bone of factor of safety S and let $U(S)$ be a cost associated with its use (taking account of the energy cost of moving the bone and of any loss of speed due to the cumbersomeness of the bone). Alexander [1] suggested that natural selection would tend to minimize a total cost $\Phi(S)$:

$$\Phi(S) = P(S).F + G(S) + U(S)$$

As the factor of safety increases, $P(S)$ falls but $G(S)$ and $U(S)$ increase. There is an optimum value of S, at which $\Phi(S)$ is least.

Ostriches are attacked by lions and other predators, from which they escape by running. The penalty for cumbersome legs may be severe, and $U(S)$ may be large for any given value of S. Moas lived in New Zealand, where there were no large predators until man arrived, so $U(S)$ may have been small for given S. This would tend to shift the optimum to higher values of S: the optimum factor of safety may have been higher for moas than for ostriches.

The calculations based on Fig. 3 showed that the stresses in the tarsometatarsi of *Pachyornis* may have been low, if it ran with small values of angle C. However, any reduction of the strength of the tarsometatarsus would have made its already thin walls even thinner, and might have made it unduly vulnerable to accidental impact. This bone needs a large diameter, to articulate satisfactorily with the tibiotarsus and the toes.

4. CONCLUSIONS

The principal conclusions of these investigations are:

(i) The stresses in the bones, tendons and muscles of the legs of ostriches, in fast running, lie in the ranges of stresses previously calculated for strenuous activities of other vertebrates.

(ii) The digital flexor tendons of ostriches store enough elastic strain energy to reduce the energy cost of running substantially.

(iii) The principal leg bones of *Pachyornis* are shorter than predicted for its (estimated) body mass, by allometric equations for flying birds.

(iv) The stresses in the leg bones of *Pachyornis*, in slow running, were probably not very high.

(v) Moa leg bones may have had unusually high optimum factors of safety, because moas were not pursued by predators.

Conclusion (i) explains nothing but supplies data that may be useful in discussions of the mechanical design of animals. Conclusion (ii) tells us something about how ostriches work. Conclusion (iii) helps us to identify those features of moa bones that require special explanation. Conclusions (iv) and (v) offer a possible explanation, in terms of selective advantage, for the robustness of *Pachyornis* leg bones.

These investigations involved fairly drastic simplifications and approximations. For example, in the study of the ostrich, many details of muscle structure were ignored: each muscle was treated simply as a collection of muscle fibres of known total cross-sectional area. Forces on the ground could not be measured directly but were estimated from the observed duty factor, in the light of force records of other species. The estimate of the strain energy stored in the digital flexor tendons was a minimum value, based on the assumption of equal stress in all the tendons. These and other simplifications and assumptions were tolerated, because the calculations could not otherwise have been made. It seemed better to attempt approximate calculations than to remain totally ignorant of the stresses, energies etc. required for quantitative understanding of the engineering design of the animal. Bone stresses calculated by such methods generally seem consistent with those inferred from experiments with surgically implanted strain gauges (data in [1]) though one recent investigation showed a disturbing discrepancy [8].

The ultimate aim of research like this must be to explain the dimensions of the parts of animals, in terms of a plausible optimality model. We are a long way from achieving this aim. Equation (1) expresses an optimality model for skeletal strength, but it has not so far been possible to quantify the functions in this equation, for any animal.

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TRENDS IN THE FUNCTIONAL MORPHOLOGY AND SENSORIMOTOR CONTROL OF FEEDING BEHAVIOR IN SALAMANDERS: AN EXAMPLE OF THE ROLE OF INTERNAL DYNAMICS IN EVOLUTION

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ABSTRACT

Organisms are self-producing and self-maintaining, or "autopoietic" systems. Therefore, the course of evolution and adaptation of an organism is strongly determined by its own internal properties, whatever role "external" selection may play. The internal properties may either act as constraints that preclude certain changes or they open new pathways: the organism canalizes its own evolution. As an example the evolution of feeding mechanisms in salamanders, especially in the lungless salamanders of the family Plethodontidae, is discussed. In this family a large variety of different feeding mechanisms is found. The authors reconstruct this evolutionary process as a series of "bifurcation points" of either constraints or opportunities forming a sequence of preconditions for the formation of a high-speed projectile tongue characteristic of tropical salamanders. Furthermore, it is shown how parallel evolution of seemingly unrelated domains within an organism such as respiratory physiology, life history biology and pattern of ontogeny has rather direct relevance to the feeding biology, thus demonstrating that organisms always evolve as wholes.

1. INTRODUCTION

In this article we present and discuss a well understood example of the interplay between structures and functions during phylogenesis. With this example we will show that the course of evolution and adaptation of an organism is strongly determined by internal morphological and physiological properties of the organisms themselves. The internal rearrangements that occur have both positive and negative implications for further evolution: they may either serve as constraints that preclude particular avenues of change, or create new opportunities. As we will see, the latter can be achieved by the formation of a new character or by modification or loss of an already existing character. The organism, therefore, as an "autopoietic", i.e. self-producing and self-maintaining system, canalizes its own evolution [11,16,26 and an der Heiden et al., this volume] .

We especially want to show how different morphological and functional parts of an organism are interrelated and how modifications in one part affect other parts that do not seem to be closely connected. In other words: the organism always acts and evolves as a whole [cf. 3,22] .

The example we present is the evolution of feeding mechanisms and feeding habits in salamanders, especially in the lungless salamanders of the family Plethodontidae, which is by far the largest, most diverse and most evolved group of urodeles.

This paper is based largely on the studies of R.E. Lombard and D.B. Wake on the functional morphology of the tongues of plethodontid salamanders, on neuroanatomical studies by the present authors on the peripheral innervation of this tongue apparatus as well as its central motor and sensory co-ordination mechanisms, and on neuroanatomical studies on the visual system of salamanders, carried out in the neuroethology research group at Bremen University, done mainly by G. Rettig, W. Grunwald and R. Linke.

2. TONGUE MECHANISMS AND RELATED ADAPTIVE PROCESSES IN SALAMANDERS

Salamanders are predators during larval and adult stages. Prey-catching behavior involves such complex neural and muscular processes as prey recognition and localization, depth perception, motor approach of the prey and final activation of the feeding apparatus and the engulfment of the prey.

In salamanders, as well as in amphibians in general, two distinct types of feeding motor responses are found: one is present in permanently or temporarily aquatic salamanders including larvae, the "Saugschnappen" or suction feeding which consists of a rapid opening of the mouth at the same moment at which the throat is expanded. This results in a rapid inflow of water including the prey item. The tongue plays only a minor role in this feeding sequence. The other type is found in terrestrial salamanders and includes a movement of the tongue out of the mouth such that the prey is caught primarily by gluing it onto the tongue pad. The terrestrial feeding responses of salamanders differ primarily with respect to the mechanisms underlying tongue protrusion and the reach of the tongue.

In most aquatic and terrestrial feeding mechanisms the hyobranchial

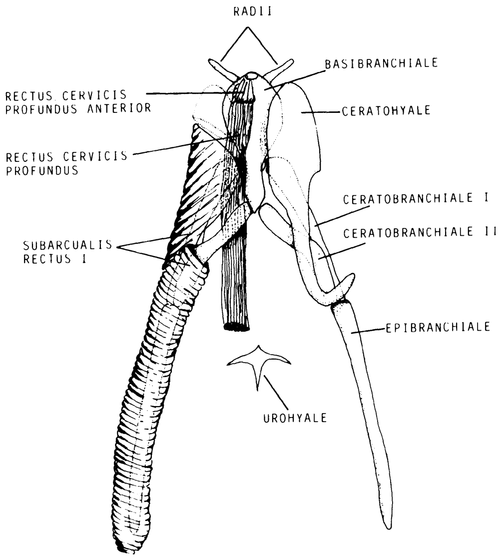

Figure 1. Tongue apparatus of the plethodontid salamander *Eurycea bislineata*. Skeletal elements are presented on the right, the main protractor and retractor muscles on the left. (After Lombard and Wake [8], modified).

apparatus plays a decisive role (cf. Fig. 1). It develops largely from the skeleton of the hyoid and branchial arches of the larvae. In salamanders of the families Plethodontidae, Salamandridae and Ambystomatidae this apparatus consists of an unpaired median basibranchial (BB) which lies in the floor of the mouth and is located far anteriorly, a short distance behind the mandibular symphysis. One to two pairs of radial elements, or radii, are attached to the anterior end of the basibranchial. Two pairs of ceratobranchials (CB) articulate with the posterior part of the BB. The first articulate with the BB near its midpoint, and the second with the BB at its posterior end. The first and second CB on each side extend posteriorly, approaching each other, and together articulate with the epibranchial (EB). The length of this latter element varies greatly among salamanders.

At each side of this apparatus a pair of ceratohyals (CH) lie in the floor of the mouth. They do not make contact with each other or with elements of the remaining hyobranchial apparatus; their posterior end is cylindrical and hooked, while the anterior portion forms a flattened blade. The CH is attached posteriorly by the hyoquadrate ligaments to the suspensorium. The final element of the apparatus is the urohyal which is the remainder of the larval second basibranchial and lies at the juncture of the rectus cervicis superficialis and geniohyoideus muscles. The tongue pad is situated at the anterior end of the BB. The BB lies in its base and the radii extend into the pad. The pad surface is covered by a large number of mucuous glands and with specialized sensory organs.

The main muscles associated with the hyobranchial skeleton are:

1. Subarcualis rectus I (SAR I). This large muscle encircles the caudal end of the EB (or first CB in those species which lack EB; see below) and extends rostrally along this element, forming a muscular sheath. More anteromedially it attaches broadly to the ventral surface of the flattened anterior part of the ceratohyals.

2. Rectus cervicis profundus (RCP). This muscle is a direct continuation of the rectus abdominis muscle and, therefore, originates from the puboischium. The muscle extends forward mediolaterally along the body axis and passes below the second CB and above the first. It enters the tongue pad inserting in various ways dorsal to the apex of the BB.

3. Subhyoideus. This muscle, when present, originates from the prosterior tip of the CH and extends anteriorly, parallel and ventral to the SARI. It inserts near the mandible on the fascia of the m. intermandibularis posterior.

4. Geniohyoideus. The geniohyoideus arises from the vertral surface of the mandible, just lateral to the symphysis, and extends posteriorly, parallel to the body axis, to the urohyal where it inserts.

5. Genioglossus. The genioglossus extends posteriorly from the ventral surface of the mandible on each side of the mandibular symphysis, above the geniohyoideus muscles, and inserts dorsally in the substance of the rostral part of the tongue.

6. Different tongue pad muscles such as the hyoglossus, basiradialis, interradialis [cf. 8].

In all generalized salamanders, the hyobranchial apparatus is involved in a dual function both in larval and metamorphosed animals: respiration and feeding. During the larval stage it serves to move the gill arches for aquatic respiration and to expand the throat during aquatic feeding or "Saugschnappen". After metamorphosis it retains both functions in those salamanders which remain permanently aquatic, or return to water for breeding. In terrestrial salamanders the hyobranchial apparatus develops as a buccal pump for respiration: the medial parts of the apparatus are drawn posteriorly and ventrally to expand the buccal cavity. Then the nostrils are closed, and the buccal cavity is constricted to force air into the lungs.

Within the family Salamandridae, three genera, *Salamandra, Chioglossa* and *Salamandrina*, have tongues specialized for feeding in terrestrial situations; all other genera have more generalized tongues, used for apprehending prey in terrestrial situations but with tongue pads that are neither strongly flipped nor projected [cf. 12].

In *Chioglossa* and *Salamandrina* the reach of the tongue is greatly extended by the very long radii and the large tongue with a free posterior flap, and additionally by the long first ceratobranchials. During forward movement of the whole hyobranchial apparatus, through contraction of the subarcualis rectus and subhyoideus muscles, the relatively massive basiradialis muscles situated inside the tongue also contract swinging the elongate radii in 180° acrs and flipping the tongue pad out of the mouth.

Within the family Plethodontidae, the genera *Desmognathus, Phaeognathus* and *Leurognathus* (subfamily Desmognathinae), have the most primitive tongue among plethodontids. Feeding is accomplished mainly by use of the jaws during rapid forward or sideward movement of the head, and only to a lesser degree of the tongue which is only slightly protruded out of the mouth (although, as in all terrestrial urodeles, the tongue makes the first physical contact with the prey). The tongue pad of these genera is relatively large and narrowly attached at its anterior margin to the floor of the mouth. Posteriorly it has a free flap of moderate size.

A more evolved tongue mechanism is found in the genera *Aneides* and *Plethodon* of the tribe Plethodontini whose members are strictly terrestrial. They possess a very large tongue pad which fills the whole intermandibular space. Although attached anteriorly, the pad has a large, free posterior flap. The tongue projection mechanisms are basically the same as in the Desmognathinae, only the tongue skeleton moves farther forward. The tongue pad is flipped out of the mouth by a complex interaction between the GG and several tongue pad muscles. The third genus of the tribe, *Ensatina*, has a more loosely attached tongue and can move its tongue skeleton rather far outside of the mouth, though it does not have a genuine projectile tongue.

Most genera of the third group, the Hemidactyliini, rely on tongue projection to capture prey. They all have small tongue pads which either are attached only loosely anteriorly or are totally free. In several genera the EB is much longer than in the previously described plethodontids so that the tongue can be moved much further forward. During forward movement, the tongue skeleton, which at rest lies spread flatly in the mouth is compressed toward the midline by a three-dimensional folding resulting in the formation of a slender, compact projectile which travels about half of its length out of the mouth. The retractor muscle, the rectus cervicis, are slightly folded which increases their length and allows the tongue to protrude out of the mouth before it is retracted by muscle contraction. In addition to the forward movement of the skeleton, the tongue pad is flipped further forward by rotation of the radii and of a lingual cartilage, a disconnected anterior process of the BB.

The most specialized tongue of all salamanders is found in the species of the tribe Bolitoglossini which all have fast, highly protrusible tongues, although the genus *Batrachoseps* has a tongue which retains a loose attachment to the lower jaw.

In the Bolitoglossini the protractor muscle of the apparatus, the SAR, has an especially elaborate form, wrapping around the long EB and forming a complex sheath. The retractor muscle may be strongly folded in the gular region. This muscle here runs uninterrupted by myocommata from the pelvic region to the anterior tip of the basibranchial, thus being greatly extendable.

As the SAR of bolitoglossines and other plethodontids with projectile tongue contracts it pulls the skeleton forward and simultaneously "squeezes" the EB out of the muscular sheath. The skeleton folds completely to a very slender projectile which is fully projected out of the mouth. Retraction is achieved by contraction of the greatly extended rectus cervicis which travels out of the mouth during tongue protraction.

In bolitoglossines the feeding apparatus evolved toward an increase in velocity, feeding distance and versatility of the tongue. Increase of velocity of tongue projection was achieved (i) by reduction of mass of the tongue skeleton, (ii) by reduction of the length of the two pairs of CB which considerably shortens the time necessary for folding the skeleton, and by shifting the main line of force transmission from the first to the second pair of CB which optimizes the track of the movable tongue during protraction [8,9] , and (iii) by full elaboration of a complete muscular sheath around the EB by the SAR muscle which wraps around the EB in a spiral way, thus being able to both pull the EB forward and "squeeze" it out.

In such a way, very high tongue protrusion velocities are reached which, as feeding reactions, may be unique among vertebrates. In some species of the genus *Bolitoglossa* the tongue is protruded out of the mouth to its full length of 20-25 mm within 2-4 ms [21]. In *Hydromantes* which possesses by far the longest tongue with a reach of 45-50 mm, the protrusion last 6-8 ms [15].

Tongue-retraction velocity is increased by a unique interaction between the protractor and retractor system. Thexton et al. [21] showed by means of electromyographic studies in *Bolitoglossa occidentalis* that the protractor SAR and the retractor RCP are activated more or less simultaneously. When both muscles contract the SAR has an advantage over RCP due to the differing length tension curves of the two muscles such that the SAR can shoot the tongue out maximally until the RCP is under full tension and draws the tongue back. After Thexton et al. the whole tongue reaction takes place in about 10 ms in *Bolitoglossa occidentalis*. In *Hydromantes* the tongue is considerably slower; it lasts 80-100 ms [15].

The evolution of such a fast, far-reaching tongue has major implications for the feeding behavior of the salamanders and especially for the visual guidance of the feeding reaction. An obvious advantage of such a feeding system is that prey can be captured which have very fast escape velocities and/or are very sensitive to approach movements of predators. The speed of the projectile tongue of most bolitoglossines is such that they can specialize on very fugitive arthropods like collembolans, as is the case in *Thorius* or *Batrachoseps* [10]. In contrast to non-bolitoglossine plethodontids as well as other salamanders which have to come rather close to their prey and have to lunge forward with their whole body to capture it, most bolitoglossini have evolved an "ambush" strategy: they wait until a prey comes within reach of the projectile tongue, and then shoot. They usually do not move their bodies forward during tongue action; they only show slow movements towards the prey before tongue projection if the prey is still out of reach.

Such a feeding strategy requires very precise depth perception. In experiments with *Hydromantes italicus* [15] and *Bolitoglossa occidentalis* [21] in which living prey were very slowly brought to the quietly sitting salamander, it was a question of 1-3 mm of further approach of the prey to elicit tongue projection. The salamanders are highly accurate, even over maximal shooting distance. This means that these animals can estimate prey distance very precisely.

The following results have been obtained concerning the visual guidance system of feeding behavior of plethodontids [14,17]:

1. Those plethodontids which possess projectile tongues have significantly more frontal eyes than those which have a less developed tongue apparatus. The most frontal eyes are found in the Bolitoglossini which also have the most evolved tongue apparatus.

2. The presence of both a projectile tongue and eye frontality is strongly correlated with the amount of so-called ipsilateral retinal input to the visual centers in the diencephalon and the midbrain. The strongest ipsilateral projections of the retina to the visual centers are again found in the Bolitoglossini.

Both features, increased eye frontality and increased number of ipsilateral retinal afferents, are commonly regarded to be prerequisites for good distance estimation. In most non-plethodontids as well as in the plethodontids without tongue specialization we find rather laterally oriented eyes and a restricted binocular visual field. In these salamanders the retina projects mostly to the contralateral visual centers in the brain. There is some ipsilateral input to visual centers in the diencephalon, but little or no ipsilateral retinal input to the main visual center, the optic tectum. In the Bolitoglossini, we not only find a broad binocular visual field, but massive ipsilateral retinal projections to the thalamus and the optic tectum. In some parts that are related to the binocular visual field, the ipsilateral retinal input equals the contralateral one.

This situation creates a complete dual projection of the binocular visual fields in both hemispheres of the brain, which can be used for very exact and fast estimation of object distance. This may be of great importance for these salamanders, because due to the relatively enormous size of the eye lenses distance estimation by means of eye accomodation seems to be difficult and/or very slow.

A final internal adaptive phenomenon related to feeding is the reorganization of the peripheral innervation of the projectile tongue. The peripheral nerves serving the tongue muscles, especially those of the tongue pad, must differ in their pathways among species having different patterns of tongue use, for biomechanical reasons, and they do [25]. For example, in the case of tongue pad flipping, where the tongue pad is fixed to the mouth and the skeleton is moved forward only slightly, there must be coiling of the nerves supplying the tongue pad, in order to supply sufficient length of the inflexible nerve to accomodate tongue pad flipping. But there is no special requirement for additional length of the nerves to accomodate the slight hyobranchial protraction. In contrast, in those species with tongue projection, where the tongue pad travels out of the mouth together with the skeleton, sometimes over a considerable distance, there must be a provision for extension of the nerves both to the tongue pad and to the projectile as a whole. The sites of coiling of the relevant nerves differ in the two groups with free tongues - Hemidactyliini and Bolitoglossini. In the former the coiling is in an anterior position, suggesting that hemidactyliines evolved from an ancestor that practiced tongue flipping. In contrast, the bolitoglossines have a posterior coiling, and the group may have evolved very early as tongue projectors from an ancestral stock which utilized only modest tongue flipping. In this regard it is interesting to recall that Wake [23] suggested that the bolitoglossines were the earliest plethodontid lineage to evolve direct development and complete terrestriality during phylogenesis (note that the question of whether direct development evolved separately in the Plethodontini and Bolitoglossini is undecided, cf. [6]).

In contrast to the situation in the periphery of the nervous system, central motor components are apparently conservative among the plethodontids. The same central coordination pattern has different effects due to differences in the biomechanically important geometry of peripheral structures having biomechanical importance (Roth and Wake, in preparation).

Finally, the development of a slender, rapid and far-reaching tongue restricts the range of possible prey types, especially because bolitoglossini usually make little use of their poorly developed jaws. While many non-bolitoglossine plethodontids and other salamanders are able to feed on large and elongate prey item like worms with the help of their large tongue and their jaws, most bolitoglossini are restricted to rather small, compact prey. This disadvantage seems to be fully compesated by the ability to feed on fast-moving prey which usually escape other salamanders, or by the possibility to invade habitats in which these types of prey are dominant, as may be the case in arboreal microhabitats.

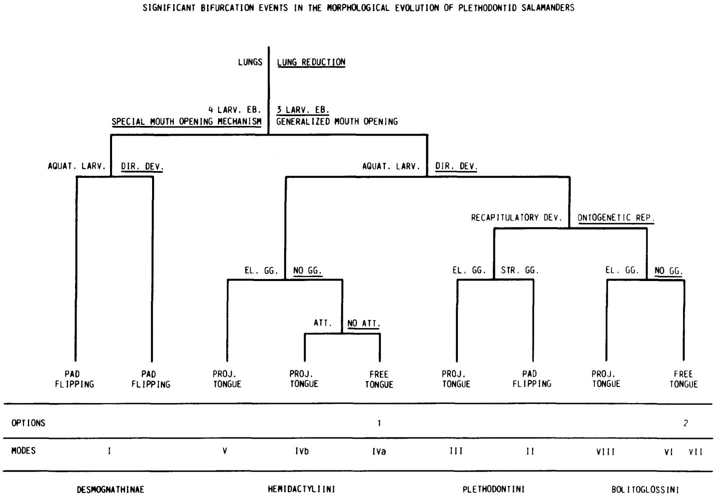

Figure 2. Schematic reconstruction of the morphological evolution of plethodontid salamanders related to feeding. All ancestral evolutionary steps are underlined. Abbreviations: LARV. EB: larval epibranchials; AQUAT. LARV.: aquatic larvae; DIR. DEV.: direct development; RECAPITULATORY DEV.: recapitulatory development; ONTOGENETIC REP.: ontogenetic repatterning; EL. GG.: elongated genioglossus muscle; NO GG.: no genioglossus; STR. GG.: strong genioglossus; ATT.: attached tongue; NO ATT.: no attached tongue; PROJ. TONGUE: projectile tongue. Numbers of "OPTIONS" and "MODES" refer to functional types of plethodontid tongues described in Lombard and Wake [9].

3. DISCUSSION

Plethodontid salamanders are an ancient group and we cannot hope to reconstruct the environments in which evolutionary processes led to the establishment of particular feeding mechanics. But we can take advantage of the diversity of living lineages and the apparently stable systems which exist today to establish a logical chain of events involving organismal-wide phenomena that have given directionality to the pattern of phylogenesis. We argue that certain historical events unrelated to feeding have had profound impact in channeling the evolution of morphology and function.

We envisage a series of bifurcations during the evolution of the family

Plethodontidae, as shown in figure 2. For the sake of argument imagine that ancient populations faced a limited set of options in confronting provincial environments. We avoid speculation as to what specific selection or other pressures might have been involved, and concentrate only on the role "decisions" made at bifurcation points have as they relate to future contingencies.

We have one bias: as phylogenesis proceeded, plethodontids generally diverged from feeding systems characteristic of generalized members of the families Salamandridae and Ambystomatidae in the directions of increase in terrestriality, and in speed, reach and mobility of the tongue.

The initial bifurcation in our scheme involves loss of lungs. The hyobranchial skeleton acts as a force pump to fill the lungs of generalized urodeles, and this imposes a powerful functional constraint on patterns of change in tongue function [24] . All terrestrial urodeles employ modest tongue projection during feeding [2,5,19] , but among the more than 325 species of urodeles there are none that have both lungs and highly projectile tongues. In contrast all species with biomechanical specialization for tongue projection either have greatly reduced and largely nonfunctional lungs, or no lungs at all.

But surely lung reduction is only a necessary, and not a sufficient, condition for the evolution of projectile tongues. There are, for example, even among the exclusively lungless plethodontids such genera as *Desmognathus* and *Aneides*, in which tongue projection is modest. While such nonplethodontids as *Salamandrina* and *Chioglossa* have highly specialized projectile tongues and greatly reduced lungs, the genera *Pachytriton* and *Rhyacotriton* also have reduced lungs but have no appreciable biomechanical specializations for tongue projection. In fact, *Pachytriton* appears to have a reduced tongue pad and to be specialized for aquatic feeding [12] . Furthermore, lung loss is not a sufficient condition for determining what particular pattern of tongue projection is produced. In the most biomechanically specialized plethodontids hyobranchial projection is featured, but in *Salamandrina* tongue pad rotation is used. Both are used by *Chioglossa*, and we speculate that lung loss in this genus might have occurred earlier during the evolution of biomechanical specialization than in *Salamandrina*, which already might have experienced a substantial reduction in the epibranchials (on which hyobranchial projection depends) by the time lung reduction commenced (it is the basibranchials and ceratobranchials that function in the air force pump).

But, for whatever reason lungs were lost in early stages of plethodontid evolution [27], this event opened an evolutionary channel leading to tongue projection that has remained open throughout plethodontid history.

The second bifurcation involves loss of a pair of epibranchials in aquatic larvae, and a probably independently derived specialization of head structure. Higher numbers of epibranchials represents the primitive condition in salamanders, and only desmognathines among plethodontids retain as many as 4 epibranchials. The extreme reduction of epibranchials has eventual important implications (see below), but the initial reduction from 4 to 3 is perhaps of little immediate functional or evolutionary significance. As with many other factors in our scheme, reduction is a necessary precondition for what later happens, and is not sufficient to force a biomechanical response. While all plethodontids with high specialization for tongue projection have 3 or fewer larval epibranchials, such genera as *Plethodon* and *Aneides* have retained rather generalized tongues. But for the desmognathines the existence of 4 larval epibranchials acts in no particularly limiting way, for very early in the history of this group the lineage became biomechanically specialized for using their heads as wedges in rocky streambeds. This specialization, which involves elaboration of bony parts, ligaments, tendons and muscles of the head and neck region, has major implications for patterns of head evolution and function [4,23]. We suspect that these changes largely preclude elaboration of morphological modifications for more than modest tongue projection.

The next major bifurcation involves evolution of direct development and it occurs in both branches of our scheme - that leading to the Desmognathinae and that leading to the Plethodontini plus Bolitoglossini. Here, again, is an event apparently unrelated to feeding which has far-reaching consequences. Surely direct development is not a sufficient condition for tongue specialization, because the direct developing species of desmognathines have not evolved beyond a stage of modest tongue projection (pad flipping) characteristic of the group as a whole. And, in contrast, the hemidactyliines, which retain aquatic larvae, include such biomechanically specialized tongue projectionists as *Eurycea*.

But, direct development is a necessary precondition for certain patterns of biomechanical evolution [9,24]. In larvae there is a strong gradient from anterior to posterior in degree of development of the ceratobranchials and epibranchials. These elements are linked by ligaments and muscles, and act as a unit in gill ventilation and suction feeding. The largest muscles attach to the largest (most anterior) skeletal elements, and forces are transmitted in chain-like fashion to the more posterior units. Furthermore, during metamorphosis feeding continues by generation of buccal suction which requires hyobranchial function. The adult epibranchial develops as a de-novo structure while the larval epibranchials are retained [20] , and during this period the ceratobranchials are the primary functional components of buccal expansion.

So in the newly metamorphosed animals life on land commences with a strong disparity in size of the ceratobranchials that is simply carried over from the larval state. Throughout life the first ceratobranchial remains the larger element and the primary force transmitter. The folding of the hyobranchial apparatus during tongue projection is determined by this size disparity [8,9] .

At first there is no biomechanical limit on tongue projection in the species with aquatic larvae, but countervening forces eventually do limit the extent to which this system evolves. The large first ceratobranchial has important implications for the efficiency of force transmission, and the hyobranchial apparatus remains relatively massive, even in highly specialized forms. So, relative to some other plethodontids, there is an eventual limitation on speed, directional versatility, and reach of the tongue tip, and the extremes achieved elsewhere are not attained.

But achievement of direct development is not a sufficient condition to overcome the limitations mentioned above, for as has been shown, direct developing desmognathines are far less specialized for tongue projection than are hemidactyliines. Further, the direct developing Plethodontini never achieve high levels of biomechanical specialization. But without loss of aquatic larvae, the opportunity for important ontogenetic alterations is limited.

The next bifurcation in our scheme separates largely recapitulative ontogenies from those in which extensive ontogenetic repatterning, including paedomorphosis in several lineages, occurs. The most evident outcome of significance for tongue evolution of following the more derived pathway is the mixing up of developmental events (what Wake [23] called differential metamorphosis, and is now generally known as dissociation), which leads in the bolitoglossines to new structural arrangements including the most elongate but also the most compact and biomechanically efficient hyobranchial apparatus. Whereas the more recapitulatory Plethodontini follow a relatively conservative ontogeny, including, for example, three developmental epibranchials of graded size despite no direct functional role for them, the bolitoglossines are freed from this apparent developmental constraint. There is a strong suggestion [23] that this group never passes through the stage of three-graded epibranchials, and the outcome is that the second ceratobranchial, when it appears during ontogeny, is larger than the first, which is reduced in size to the point that it no longer plays an important biomechanical role in tongue projection [9].

There is a second possible implication of ontogenetic repatterning, or at least of direct development (on which the possibility of ontogenetic repatterning itself depends). Plethodontids as a group differ from other salamanders that have been studied in the degree of eye frontality and the presence of ipsilateral projections from the retina to the optic tectum. However, within plethodontids there is a clear association between the elaboration of these factors and the loss of aquatic larvae. In larvae the eyes have a strongly lateral orientation and almost no ipsilateral fibers to the central visual system are present. During metamorphosis, as in amphibians in general, the eyes undergo some forward migration, and a few ipsilateral fibers are established, mostly to the diencephalon rather than to the tectum. However, in the bolitoglossines eye frontality is pronounced, and the degree of ipsilaterality is greatly increased [14]. These factors, which are of considerable significance in the achievement of binocularity, which in turn has obvious relevance to feeding by tongue projection, do not become well developed without the loss of larvae, but since they are no better developed in the Plethodontini than in the Hemidactyliini, we suspect that the more general level of ontogenetic repatterning achieved by the bolitoglossines is a necessary precondition.

The final level of bifurcation in our scheme is the only one that has an apparent direct relevance to tongue projection. The genioglossus muscles attach the anterior part of the tongue to the lower jaw at the mandibular symphysis, and so long as they are present the tongue cannot be truly free. But even in this case there are important contingencies. Thus, in three entirely separate lineages (represented by the genera *Hemidactylium*-Hemidactyliini, *Ensatina*-Plethodontini, and *Batrachoseps*-Bolitoglossini the genioglossus has undergone a shift in orientation and a modification in structure which permits but does not facilitate substantially more tongue projection than occurs in other plethodontids which retain the muscles.

An extreme is reached in *Batrachoseps* in which the muscle is so slender and elongated that it inserts near the posterior end of the mandible [13]. Alternatively, in the hemydactyliine genera *Typhlotriton* and *Stereochilus* the genioglossus is reduced to a few fibers or is absent, but a fleshy (fibrous connective tissue and epithelium) attachment connects the tongue to the anterior floor of the mouth. Nevertheless, in order to attain a truly free and projectile tongue, the genioglossus muscles and the fleshy attachments both must disappear.

The options taken at this final bifurcation have implications, and each has an apparent stopping point imposed either by this event or some prior one. Thus *Batrachoseps* entered a channel which led to very great specialization of the genioglossus and substantial projectile capacity, but nevertheless left it with an attached tongue and an apparently closed evolutionary channel. We have already discussed the stopping point reached by the hemidactyliines. The stopping point of the two free-tongued bolitoglossine supergenera (*Hydromantes, Bolitoglossa*) is more speculative because of our knowledge of the existence of two morphological states which we could not have predicted from biomechanical considerations related to the theoretical model of Lombard and Wake [8].

First, in *Hydromantes* an unexpected lengthening of the basibranchial occurred in conjunction with a very great lengthening of the epibranchials, associated with increased reach of the tongue. Basibranchial length bears a near isometric relationship to body length in all other plethodontids, and this new relationship could not be predicted. Secondly, in *Thorius* and possibly some other tiny members of the supergenus *Bolitoglossa* the first ceratobranchial is so reduced in size that the anterior attachment is weakened and the normally articulated hyobranchial apparatus disarticulates during projection, thus at least in theory increasing the mechanical efficiency of the system. Again, this was not predictable, and in fact Lombard and Wake [8] accepted articulation as a premise in developing their biomechanical model. The occurrence of these two extremes of specialization should caution against further prediction that bolitoglossines have reached a morphological stopping point, although we think it likely (but we could be accused of failure of imagination!).

4. CONCLUSIONS

Our goal for this essay has been to demonstrate with an empirical example what we believe to be a principle of phylogenesis. There is an unfortunate modern tendency to ignore what we consider to be internal factors in evolution, such as the various constraints that restrict phylogenetic diversification, and the factors which, in contrast, open what are essentially organismal (i.e., developmental, morphological, physiological, behavioral) channels along which evolution appears to move with directionality, following avenues of least resistance. But the existence of such channels does not ensure a particular pathway. Rather, some organismal phenomenon is a necessary precondition for a particular pattern, or subpattern within an overall pattern of parallel evolution. In the case we have chosen, the parallel evolution of feeding systems utilizing projection of free tongues in plethodontid salamanders, such seemingly remote phenomena as respiratory physiology, life history biology, and pattern of ontogeny have been shown to have rather direct relevance to the feeding biology, including such diverse components as sensory perception and biomechanics. This paper is an attempt to reintroduce a strongly organismal component to considerations of evolution and phylogeny, such as we have advocated elsewhere [7,26] .

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QUALITATIVE AND QUANTITATIVE EXPLANATION OF THE FORMS OF HEAT SENSITIVE ORGANS IN SNAKES

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ABSTRACT

Heat sensitive pit organs in different species of snakes show various shapes. The relation between form characters and functions were analysed by means of two different research programs. This paper presents the methodological steps involved in these research programs. The first approach is called a qualitative explanation because it connects experimental data by means of qualitative statements in order to give a functional morphological explanation for the construction of the pits in respect to the behaviour of the snake. The second approach is called a quantitative explanation because the core of the explanation is a mathematical model which in its consequences explaines the construction of the pits in respect to image formation.

1. INTRODUCTION

The present volume aims the presentation and discussion of different methodological approaches in the field of functional morphology. I selected for that goal two examples from my own work [4,5]. Both deal with the question to what extent the variation in forms of heat sensitive pit organs in snakes are related to different functions.

Pit organs are depressions (1-3 mm deep) in various shapes situated on the upper or lower lip of Pythoninae and Crotalinae. These, by their pink colour of the floor, contrasting pits are known since the fifties to be heat sensitive organs [1].

This paper presents two successive attempts to elucidate the form-function relationships in the labial pits of *Python reticulatus* and in the facial pits in Crotalinae.

2. THE QUALITATIVE EXPLANATION

In order to elucidate the relation between the various forms of the pits and their functional significance, a description of the anatomy and the functions in necessary. The description of the anatomy includes not only the epidermal construction of the receptive areas but also the capillary system of the head and the related connections of the peripheral nerves with the connections in the central nervous system. The features which are shared by all types of pits are the shape, size and positiong of the receptors. The receptors are groups of 5-8 bulbus nerve endings (each 50 µm diameter) packed with mitochondria just 5-10 µm beneath the surface of the pitfloor. A section through this area shows few, if any epidermal cells, only a dense layer of these non-myelinated nerve endings and blood capillaries. The pink appearance of these sense organs from the outside is due to the large number of capillary loops protruding very close to the surface. Branches of about 400 myelinated nerve fibres (2.5-6.4 µm diameter) descend from each labial pit to the central nervous system.

According to the "method of concomitant variation" [7,13] the mutual differences in forms in relation to concomitant functions are of more interest than the shared ones. There is an obvious difference between the labial pits in the upper lip and those in the lower lip, see Fig. 1. The shape of the pits in the upper lip is, in all the species of Pythoninae, vertically elongated: oval, sickle or triangular with the base dorsally. The pits projecting ahead are deeper than those projecting aside. The number of pits varies in different species between two, in the first supralabial scales, to 10 in the successive 5 labial scales on both sides of the head. Those in the lower lip are round or square, never vertically elongated. In contrast to the upper lip the caudal pits are generally deeper. The pit floor is deepest in the middle. The number of infralabial pits varies between 6-20. All the pits in the lower lip are innervated by the mandibular branch of the nervus trigeminus. The pits in the first scales of the upper lip are innervated by the ophthalmic branch and the other pits in the upper lip by the maxillary branch of the nervus trigeminus.

In the medulla, the first relay station in the central nervous system, the projections from the three different branches are still topographically distinguishable [14]. However, at the level of the next integration station, the tectum mesencephali, the projection areas of the mandibular and maxillary

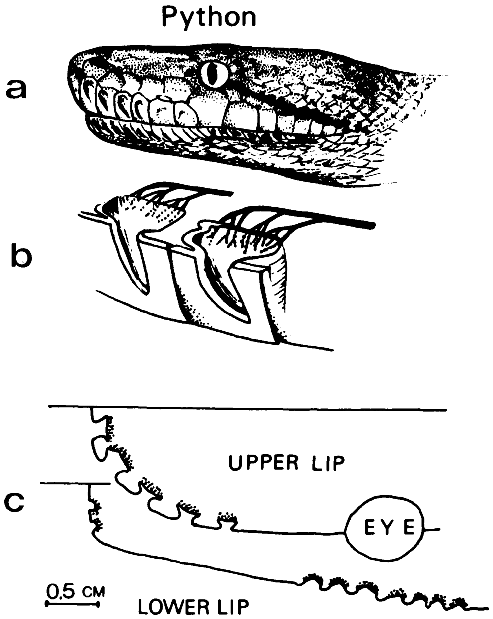

Figure 1. (a) Head of *Python reticulatus*. (b) Detail of a supralabial pit and its innervation. (c) Horizontal sections through the upper and lower lip. Sensitive parts are dotted.

branches overlap considerably [11,15]. The ophthalmic branch projects exclusively bilateral to the anterior part of the tectum.

Early experiments by Ross [17] and Noble and Schmidt [16] established the relation of these organs with the hunting behaviour. However, detailed analysis is necessary to describe the precise situations in which heat information appears as an important, a necessary, or even better, a sufficient condition to enrole normal hunting behaviour. This question asks for a detailed description of the "normal" behaviour.

Normal hunting behaviour can arbitrarily be divided into nine phases based on locomotory criteria. (1) *Rest*: The snake is coiled up with a contracted pupil. (2) *Alertness*: Although the posture does not change, the pupil enlarges and tongue flicks can be observed. (3) *Head turnings*: The snake points its head towards the stimulus. The pupil becomes larger and tongue flicks appear more often. (4) *Approach*: The snake starts crawling toward the direction of the stimulus while frequently flicking with the tongue. The pupil maximally enlarges depending on the light conditions. (5) *Preparation*: At close distance of the stimulus (10-20cm) the anterior part of the body is drawn in an S-shaped curve while keeping the head at the same position from the stimulus. (6) *Strike*: In a sudden fast movement the snake injects the prey with poison. (7) *Constriction*: In the same darting movement a U-shaped loop is coiled around the prey, followed by several additonal coils. When the prey does not move the constriction lasts maximally 3 minutes. (8) *Head searching*: The coils and the fangs are released followed by several sweeping movements of the snout between the anterior and posterior part of the strangled prey over the surface or in the fur, of the prey. The last behavioural phase before returning to rest is (9) *Swallowing*. Most often the prey is swallowed with the anterior side first. Swallowing starts with an alternating caudal movement of the pterygoids which possess long rows of teeth. When the first part of the prey reaches the esophagus, movements of the muscles in the neck and the peristalsis of the esophagus draw the object down to the stomach.

In order to determine whether heat information is an important, necessary and/or sufficient condition to enrole normal hunting behaviour, one has (a) to analyse each of the nine behavioural phases, and that (b) in context with the other sensory information channels. Regarding the first demand (a), it must be realized that the nine behavioural phases are arbitrarily chosen on locomotory grounds, which implies that none of the behavioural phases can be analysed as a functionally isolated part of the hunting sequence. Furthermore, every phase is largely predetermined by the earlier behavioural phase(s). The second demand is necessary to avoid the pitfall in which no measurable change in impact of heat information is observed on the behaviour, while the impact of other sensory information might change considerably at the same time. This approach is far from the well known and frequently applied behavioural design in which strong reduction of parameters results in statements dealing about one specific behavioural phase of the entire hunting sequence and about one specific sensory system.

Again, based on the method of concomitant variation, a systematic variation in sensory stimuli was presented to the snake and the concomitant changes in the hunting behaviour were noted. The following were selected as relevant sensory stimuli: optical stimulation (vision, eye); infrared stimulation (heat, pit organs); chemical stimulation (smell, Jacobson organ, nasal cavity) and mechanical stimulation (vibration, touch receptors

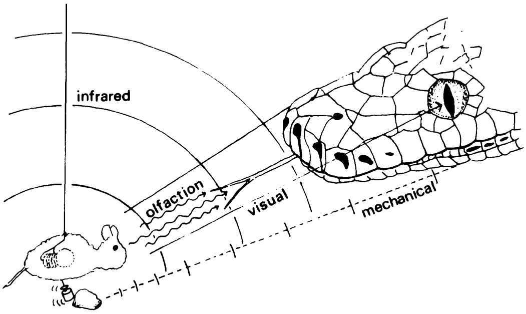

Figure 2. Artificial stimulus carrying four stimuli: heat, mouse odour, mechanical vibrations and optic stimuli.

in the body wall).

Introduction of changes in the sensory environment of an animal can be done either by blocking the sensory organs of the animal or by selectively stimulating the animal. In the first case the stimulus can be a natural prey object, but the snake shows a behaviour which is influenced to an unknown degree by the handling of the investigator and the devices which block the sensory organ(s). In the second case the snake does not have to be handled, but the stimulus is artificial, e.g. an artificial mouse with a heating element in its core, added mouse odour and a dragging weight to induce floor vibrations, see Fig. 2. The first method is also limited by the fact that only the eyes and the pits can be blocked in a reversible way. The second approach, on the contrary, meets only marginal creative problems in designing non-visual stimuli: like stimuli not added to the core of an artificial cotton mouse [3,5] : only smell, fibration or heat. The range of the conclusions are of course prescribed by these practical boundary conditions of the experiments. The second method, using single, double, triple or all of the four stimuli, is most suitable to trace the minimal set of stimuli which induces and/or maintains the hunting sequence. The first method of blocking vision and/or heat deals always with the two open information channels smell and touch, and therefore is only capable of detecting sub-optimal behaviour when the hunting sequence is already on its way.

From these experiments the conclusion was drawn [5] that the most important and even sufficient stimulus to start and to maintain the hunting sequence is an optical stimulation in *Python reticulatus*. Heat information plays only a secondary role in the alertness phase, the preparation and strike phase.

Now that the anatomy and the behaviour are described, the relation between form and function can be established by means of the method of functional-morphological deduction [8]. There are three successive steps.

I. Translate the relevant parts of the behaviour into a technical vocabulary indicating the functional conditions which have to be met to enrole these parts of the behaviour.

II. Transformation of these functional conditions into a form condition (shape, size, position) by means of physical and/or technical laws and principles.

III. Evaluation of the comparison between the formulated form-conditions and the actual anatomical features in the animal.

In the first step the behavioural phases, alertness, preparation and strike can be translated into the following more abstract functional conditions: In the case of the alertness phase, relatively long range sensitivity, not necessarily linked with high angular resolution, and for the preparation and strike phase, relative short range sensitivity with high angular resolution.

In the second step radiation laws are used to transform "long range" and "short range" into larger and smaller sensitive areas. Geometry can be used to transform the conditions low and high angular resolution into shallow and deep pits or wide and narrow pinhole cameras.

The third step leads to the construction of an intuitively sound model which explains some of the overt form features (Fig. 3). The large number of pits in pythons are related in this way to the alarm function to warn the snake for danger or prey. The supralabial pits with their relative small opening, wider sensitive floor and the deepest pits projecting right ahead, are perfectly well apt to locate the prey in the last moments preceding the strike. The evaluation, however, shows also the incapability to explain the different forms of pit openings, the different positioning of the sensitve floors (flat or curved) and the amount of blood capillaries.

Some *ad-hoc* explanations can be added to complete the model. It is obvious that the elongation of the supralabial pits which runs down towards the rim of the upper lip does not contain thermoreceptors. This might indicate a totally different function. An alternative might be that this construction gives way to water which otherwise will stick into the

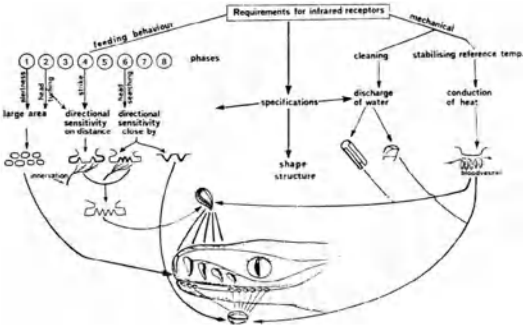

Figure 3. Relation between functional demands and the construction of the labial pits.

deep pit when the snake rises out of the water. This problem is absent in the shallow pits of the lower lip. Simple tests with a droplet water confirmed this hypothesis. I call this explanation QUALITATIVE, because the physics involved in order to relate anatomical and behavioural data leads to qualitative statements. Consequently a qualitative explanation which connects two in principle falsifiable research programs in anatomy and behaviour can never stand Popper's criteria of falsification. Critics might remark that it is "natural history", "just a story" or "nothing more than an appealing construction". I would call it a "good start" which generates several challenging opportunities to construct a QUANTITATIVE explanation relating separate fields of research.

3. THE QUANTITATIVE EXPLANATION

Since the beginning of the fifties extensive research on the neurophysiology and neuro-anatomy of the heat sensitive system in pit vipers offered a huge amount of data which were not related to each other in a consistent mathematical model. On the contrary, the neurophysiological characteristics of the heat receptors described by various researchers showed as many differences. An interesting dispute about the existence of lateral inhibitory fields separated the opinions of a Japanese research group working with the Asian pit viper *Agkistrodon blomhoffi* from the American research group doing experiments with the American pit viper

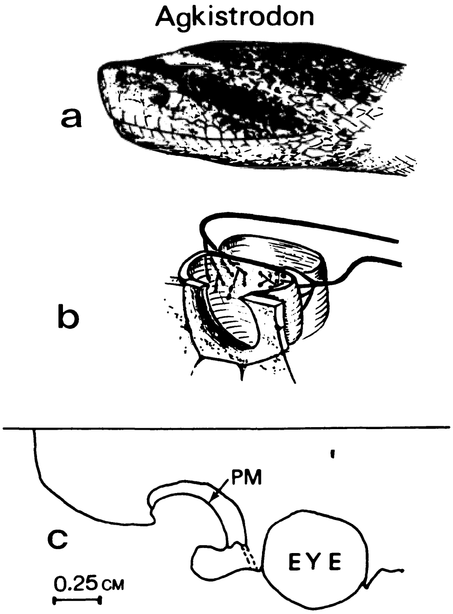

Figure 4. (a) Head of a crotalid. (b) Detail of the facial pit and its innervation. (c) Horizontal section through the head showing the sensitive pit membrane (PM).

Crotalus viridis. The last group collected strong evidence in favour of a spatial inhibitory field just lateral to a related excitatory field by showing that simultaneous stimulation by two heat sources in the centres of the described excitatory and inhibitory fields resulted in the extinction of the neural excitatory activity. On the other hand, the Japanese group never found a related inhibitory area adjacent to an excitatory area while scanning the heat sensitive pitfloor with a tiny red light laser spot of 50 μm diameter. The dispute was settled for the time being, as species difference.

Before entering into the construction and profits of the mathematical model a brief introduction into the anatomy of the heat sensitive *facial* pit in crotalids is in place. All pit vipers possess a single pit on each side of the head which is positioned between the eye and the nostril (see Fig. 4). The highly vasculated floor of the facial pit is actually a thin membrane (15 μm thick) suspended over an underlying cavity. There is only little variation in form aspects between the species. This pit membrane is

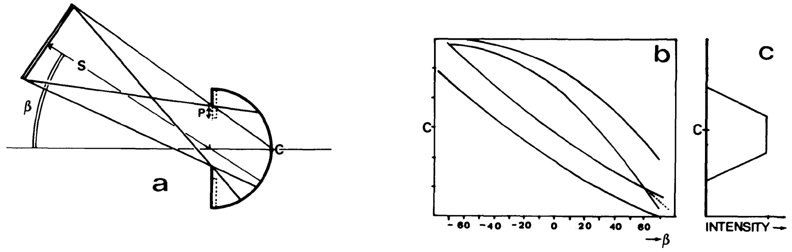

Figure 5. (a) Geometrical construction of the projected image (B angle of incidence). (b) Graphical representation of the image as a function of the angle of incidence (C= center of the pit membrane). (c) Intensity distribution of the projected image at a given angle of incidence.

innervated by ca. 6000 myelinated fibres (2.5-3.5 µm diameter) belonging to the maxillary and ophthalmic branches of the trigeminus system. Each receptor unit contains several bulbs filled with mitochondria and measures approx. 40 µm in diameter [2,22] . Centrally the heat information is successively transmitted to three integration levels: the medullar LTTD nucleus [18] collecting information from a receptive area of 360-800 µm diameter [21] , the nucleus caloris reticularis [12,19] and the stratum griseum centrale of the mesencephalic tectum [9,10,20] collecting information from a receptive area of 500-1000 µm diameter.

In the quantitative approach the shape of the facial pit is reduced toward a half circular pit membrane and an aperture shifted slightly rostrally, see Fig. 5a. In contrast to a point source, a radiating object with a given extension at a given distance projects an image which possesses a central part with high intensity and a surround with decreasing intensity (see Fig. 5c). The positions of the borders of the central and surround parts can be calculated by means of goniometry. The next step is to extend these goniometric formulas as a function of the position of the radiating object in respect to the facial pit, as a function of the angle of incidence. The projected positions of these borders on the pit floor can be graphically depicted (Fig. 5b) as a function of the angle of incidence.

This mathematical model enables us to simulate all the described experiments in the literature. Filling in the anatomical data (aperture, pit depth, receptive area) and the experimental data of the stimulus source (distance, diameter, radiation intensity) one can predict in what part of the surrounding space a response will be evoked. Adding neurophysiological data concerning radiation intensity and neural responses, extends the

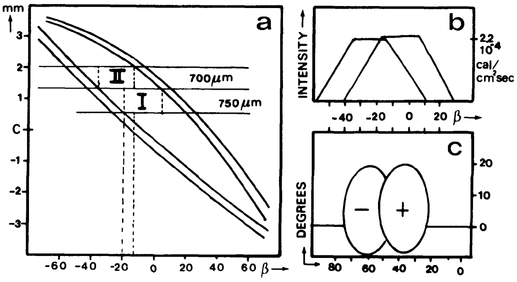

Figure 6. (a) Theoretical position on the pit membrane of the excitatory area (I) and inhibitory area (II). (b) Amount of illumination received by area I and II, plotted as a function of the angle of incidence. (c) The experimentally delineated excitatory and inhibitory fields. Azimuth and elevation are indicated according the original data.

predictions to the amount of neural response at every desired angle of incidence, which is, in fact, a direct falsifiable test situation.

In the same way the model can be used to simulate the experiments which led to the dispute about inhibitory field. Filling in the anatomical and experimental data one can easily calculate where the excitatory and inhibitory areas, if any, have to be located on the pit membrane. The solution (Fig. 6) makes clear why the Japanese group never could, and never will, find the inhibitory area. There are, indeed, two adjacent receptive areas: (I) excitatory, 750 μm in diameter, and (II) inhibitory, 700 μm in diameter. But the second order neuron responds only when both areas are simultaneously radiated and with a dominant excitatory response over the inhibitory response. In other words, when the pit membrane is scanned by a 50 μm spot either the inhibitory area is radiated or the excitatory, and consequently this specific second order neuron will never respond. Conclusion: no species difference is necessary as an escape-hypothesis, only a methodological difference must be accepted.

The simulations, predictions and evaluations with the experimental data revealed an interesting consequence regarding the three levels of sensory information integration. As mentioned before, it was known that higher order neurons are connected with larger areas of receptors. And all these areas show extensive overlap with each other. Fig. 7 depicts the projected radiation image for a given ratio object diameter and stimulus distance. Most often this image shows a trapezoid intensity distribution with a central part receiving maximal intensity, a surround part with decreasing

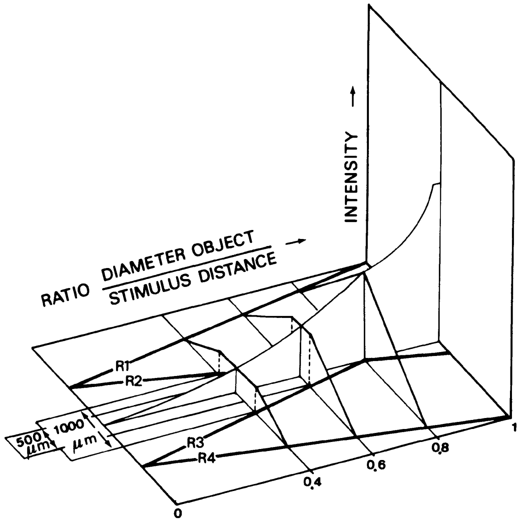

Figure 7. General relation between the ratio of object diameter to stimulus distance (O/S), and the diameter of the central and surround part of the projected image on the pit floor. Vertically the intensity as a function of the inverse square of the distance is superimposed.

intensity. However, when the object is brought closer to the pit, at certain distance the trapezoid intensity distribution changes into a triangular shape, which means that there will be a receptor which only responds maximally when the stimulus radiates from one specific place in space: high angular resolution. The same triangular situation occurs for higher order neurons when the central part of the intensity distribution has the same diameter as the connected area of receptors (resp. 360-800 µm and 500-1000 µm diameter). This means that the high spatial resolution is extended to the left side of the diagram, to larger distances. In other words, the centre of a mouse is exactly located up to 14 cm distance, which is within the actual strike distance.

As mentioned just before, the centre of the object is spotted, not the edges, at least at the level of the tectum. This is not without profit when it is realized that the central image always possesses the maximal radiation energy. If this model is rightly interpreted, the shape of the edges of the pits are of minor importance for this system. In other words, the shape of the pit is not of direct importance for the heat sensitive system.

Other functional demands might have their influence on the actual shape.

In analogy with the mathematical model of the pit vipers, a first attempt was made to characterize neurophysiologically the heat receptors in *Python reticulatus* [6] which brought to light an essentially different type of heat receptor than in crotalids. One, in python the functional receptive area is approximately 150-250 μm in diameter (in crotalids 50 μm). Two, the absence of background activity and responding to both heat and touch (in crotalids temperature dependent background discharge; only responding to heat). The response to a stimulus is phasic and fast adapting without a consistent relation to the stimulus intensity or duration (in crotalids an obvious relation between stimulus intensity and burst shape).

At this moment no experiments are available which could test a similar model against experimental data. However, when one realizes that (a) the tectal organization of the visual and heat sensitive projections are equal in pythons and crotalids. And (b) that the output of the visual system towards the tectum must match functionally with the output of the trigeminal heat sensitive system towards the tectum, then it will be obvious that the peripheral differences between the heat receptors and pit structures in pythons and crotalids are a clear example of two different solutions for the same functional demand: hunting prey by means of heat information.

4. CONCLUSIONS

Both presented approaches appear to be fruitful to solve functional morphological questions. The status of the models used during the research programs are, however, quite different. In the first (qualitative) approach the ultimate goal was to develop a model (model = a qualitative description of relations between pits and behaviour) by means of experimental data. In the second (quantitative) approach the mathematical core of the model (model = a mathematical relation between image formation and the construction of the pit) was given, which in its consequences explains functional morphological relations.

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PROPORTIONS OF THE JAW MECHANISM OF CICHLID FISHES CHANGES AND THEIR MEANING

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ABSTRACT

The jaw mechanism of cichlid fishes is an intricate apparatus with complex force transmission from muscles to environment. The proportions of this apparatus change considerably during growth mainly due to scale effects. In adult fishes, the proportions differ, corresponding with the type of preferred food. In such a complex mechanism, it is very hard to gain insight into the functional meaning of the differences in proportions, unless a biomechanical model is constructed, describing kinematics and force equilibria of the apparatus.

Such a model has been constructed and by means of perturbation analysis anatomical points could be selected of which the positions are very important for the function of biting. These "hot spots" need only small displacements in order to obtain an increase in biting force. By means of a newly developed mathematical technique, it was possible to move the anatomical points in very small steps towards more favourable positions for the function of biting.

In this way, an improved version of an existing not very powerful biting insect feeding species, *Haplochromis elegans*, was calculated. This calculated version resembles a more powerful biting species *Haplochromis nigricans* very closely. Also, the functional meaning of the proportional changes during growth of the insect feeding *Haplochromis elegans* could be evaluated. In both cases compromises could be indicated where functional demands are in conflict with each other on the level of the anatomical design of the jaw mechanism.

1. INTRODUCTION

In general, one encounters two approaches in finding the relation between form and function of a particular functional component (sensu [4]), when functional morphological studies are surveyed.

The first approach starts with one particular species. A numerical model is formulated or some other set of consistent reasoning from which predictions can be made. These predictions can be made starting out from functional demands towards the formparameters [4] or from formparameters towards the functional characteristics [9]. The model or theory can be improved by testing the predictions in a trial-and-error cycle. When the model is sufficiently corroborated, it can be occupied to evaluate differences in several species.

The second approach compares a number of species with differences in the functional component under investigation. From these differences, laws are induced which could describe the relation between form and function.

However, in both approaches the actual changes in the functional component that may occur in ontogeny or phylogeny are neither directly studied, nor simulated, nor understood. This lacuna can be filled in by using a numerical model as a to be optimised system, by stating the desired changes in the functional demands.[1] In the present study, this approach will be demonstrated for the jaw mechanism of cichlid fishes.

2. METHODOLOGY

1) From the approximately 300 haplochromine species, *Haplochromis elegans* was selected, because of its morphological central position in this species flock [1,5].

2) The jaw apparatus was selected as an interesting functional component.

3) This apparatus was recognized to be a complex mechanism.

4) From this apparatus, the essential anatomical information was selected which constitutes the mechanism, such as joints, points of insertion, etc.

5) This anatomy was simplified, leaving only the kinematical properties.

6) The kinematical properties of the connections between the bones, connective tissue and muscles were described in mathematical terms.

7) A biomechanical model was constructed of the jaw mechanism, employing the information from 5) and 6).

8) The movements of the mechanism were calculated.

9) They were compared with the actual movements obtained from film analyses and positions in serial sections.

10) Force equilibria were calculated during biting and protrusion of the upper jaw.

Then three lines of methodology were followed:

I. Comparison of ontogenetic stages of *H. elegans*.

II. Indication of "hot spots" in the design of the jaw apparatus of adult *H. elegans*.

III. Design of an improved version of *H. elegans* with respect to biting force and comparison with a powerful biting cichlid species.

I. Comparison of ontogenetic stages of *H. elegans*.

I.1. The earliest ontogenetic stage of *H. elegans* was selected which had a complete jaw mechanism.

I.2. The anatomy of this stage was abstracted, put in the model and evaluated in terms of the force transmission during biting.

I.3. This force transmission was compared with the transmission in the adult stage.

I.4. By means of perturbation analysis (see lines II and III and the appendix) it was decided which anatomical features produced an increase in biting force and which ones not.

II. Indication of "hot spots" in the design of the jaw apparatus of adult *H. elegans*.

II.1. The anatomical points of adult *H. elegans* were all moved slightly in three orthogonal directions one after the other.

II.2. From the effects these displacements had on the biting force transmission, the ones that produced the highest increase in biting force were selected. These are called the "hot spots".

III. Design of an improved version of *H. elegans* with respect of biting force and comparison with a powerful biting haplochromine species.

III.1. The anatomical points of adult *H. elegans* were all moved slightly in three orthogonal directions one after the other, with replacement of the last one that was moved.

III.2. From the effects these displacements had on the biting force transmission, the optimal directions were calculated in which the "hot spots" should move in order to increase the biting force with the least amount of morphological change.

III.3. By repeating III.1 and III.2 several times, a new configuration of the jaw mechanism was calculated with a highly improved biting force transmission.

III.4. This improved version was compared with *H. nigricans*, a powerful biting haplochromine species, and found to be a correct prediction in six out of the seven changes predicted.

III.5. The incorrectly predicted change could be related to the existence of a functional compromise between eating and respiration or vision (see section "Results" under III).

3. MATERIAL AND TECHNIQUES

Wild caught specimens of *Haplochromis elegans* and *Haplochromis nigricans* were used to produce epon embedded serial sections. Ontogenetic stages of *H. elegans* were obtained from adults living in watertanks and embedded in epon for the preparation of serial sections.

The shape of the articulation surfaces and the positions of relevant anatomical points were measured by means of a Nikon Profile Projector.

The kinematical and statical calculations were performed with an algorithm written in APL and operated on an IBM 370 computer with VERSATEC graphic output.

4. RESULTS

From the jaw mechanism of *Haplochromis elegans* a numerical model was made, describing both the kinematics and the statics. Figure 1 shows a reconstruction of the jaw mechanism in a young specimen of *H. elegans*, the first free-swimming stage of this mouth-brooding species.

The movements of the bony elements in space as calculated by the model were compared with the actual movements by means of filmanalyses and serial sections of specimens that were embedded in different phases of head expansion and mouth opening. The seventh version of the model proved to predict the movements sufficiently accurately. Since then, the jaw mechanism was described satisfactorily (points 1 through 10 of the section on methodology), the model was open for use in studying proportional changes.

I. Comparison of ontogenetic stages of *H. elegans*.

The earliest ontogenetic stage of *H. elegans* was selected which already had a complete jaw mechanism. This stage was also the first free-swimming stage (figure 1). The anatomy of this stage was abstracted and fed into the model. The output of the model was compared with that of the adult.

Although the proportions of the head skeleton are widely different, including those of the jaw apparatus, the force ratio of the adductor muscle of the upper jaw to that of the biting force at the most rostral

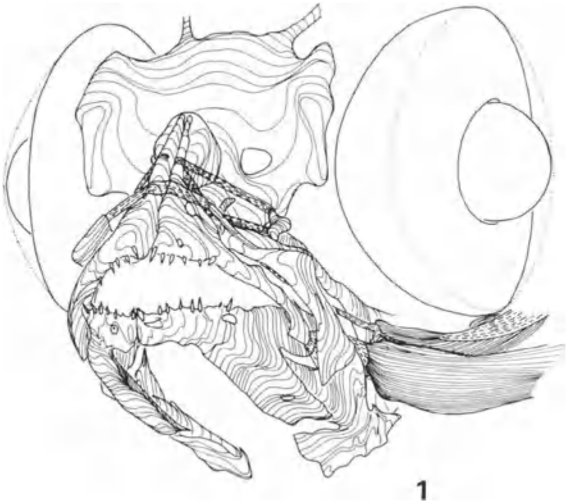


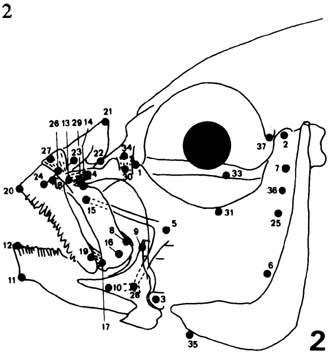
Figure 1. Oblique frontal view reconstruction of the jaw apparatus of a first free-swimming stage of *H. elegans*. Qualitatively, the apparatus is the same as in the adult, only the proportions differ.

teeth was about the same as in the adult. After a perturbation analysis (see appendix and section on methodology) was performed, I decided which anatomical proportions were favourable and which ones unfavourable for a high biting force in the young stage. The relative short and steep upper jaw in this stage were favourable conditions. The short coronoid process of the lower jaw was also favourable. The presence of a relatively large eye (figure 1) in the young stage proved to be unfavourable for a high biting force. However, the favourable conditions nullify the effect of the large eye on biting force, which is why the biting force transmission is about equal in the young stage and the adult.

II. Indication of "hot spots" in the design of the jaw mechanism of adult *H. elegans*.

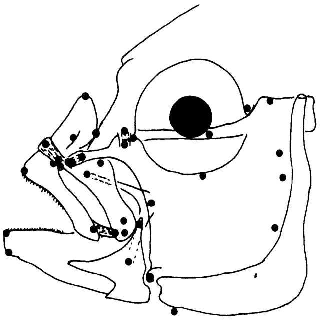
After I sequentially perturbed the positions of all anatomical points (see appendix), seven of these points could be indicated of which small displacements resulted in noticeable changes in the biting force transmission. They were:

1. Shortening of the premaxillary ascending arm (20,21).
2. Steepening of the premaxillary ascending arm (20,21).



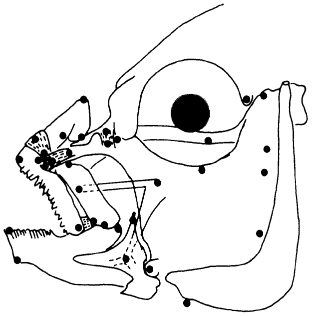
2A

H. elegans



2C

H. nigricans



2B

H. elegans with improved proportions for biting

Figure 2A. Anatomical points selected in adult *H. elegans*, constituting the kinematical model and subject to perturbation analysis.
Figure 2B. Adult *H. elegans* after improving the biting force by changing the proportions on the basis of perturbation analysis.
Figure 2C. The positions of the anatomical points of *H. nigricans*, an algae scraping species. Six of the seven proportional changes encountered in the improved version of *H. elegans* are found in this species.

3. Rostrad movement of the intermaxillary ligament relative to the maxilla (26).

4. Lengthening of the maxillad process of the palatine (4).

5. Shortening of the coronoid process of the dentary (8).

6. Dorsad shift of the adductor muscle of the upper jaw, resulting in a smaller eye or displacement of the eye (5).

7. Caudo-ventrad shift of the insertion of the adductor muscle of the upper jaw on the maxilla (15).

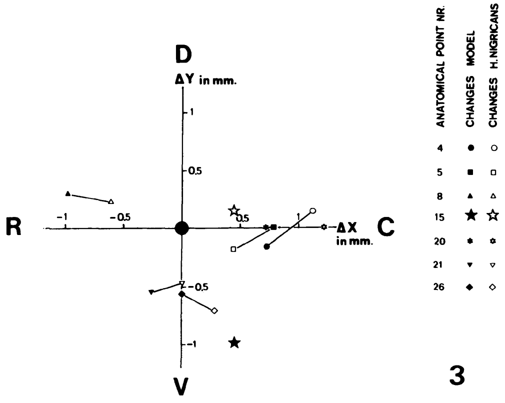
The numbers in brackets refer to the anatomical points indicated in figure 2A. If the jaw mechanism needs to have a higher biting force, with a minimum of anatomical change, these seven changes have to be made first. The anatomical points of which the positions have to be changed to make the biting force higher, are called the "hot spots" of the jaw apparatus.

III. Design of an improved version of *H. elegans* with respect to biting force and comparison with a powerful biting cichlid species.

The perturbation analysis was performed on adult *H. elegans* and after each analysis, the most important point was selected and displaced in the most effective direction (see appendix). This procedure was repeated many times, resulting in an improved version of *H. elegans* with respect to biting force transmission (figure 2B). The procedure was stopped when the changes were noticeable, but remained within the form variation encountered amongst haplochromine fish.^{2}

The resulting improved version was compared with *H. nigricans*, a species from Lake Victoria, which grazes on algae from rock. This species has a 60 % larger cross sectional area of the adductor muscle of the upper jaw than that in a specimen of *H. elegans* of the same size, indicating that it is a specialised biting species relative to *H. elegans*. The anatomical points of *H. nigricans* have been given in figure 2C. Using *H. elegans* as a reference, the changes in position of the seven anatomical points which had the largest displacements were plotted in a parasagittal projection (figure 3). This has been done for the improved version as depicted in figure 2B as produced by the mathematical operations as well as for *H. nigricans* pictured in figure 2C. The large black dot on the origin of the coordinate system represents *H. elegans*. As can be seen, all points have displacements that are similar in direction and magnitude in both the improved version of *H. elegans* and the natural version of *H. nigricans*. Point number 15 however, indicated with the bigger symbols of open and filled stars, has a very different direction and magnitude of displacement. This point determines the direction of the tendon of the adductor muscle of the upper jaw and the place of insertion of this tendon on the maxilla.

A suggestion will be given here why the position of this point was not predicted correctly. At a given maxillary swing during mouth opening, the muscle fibers of the adductor muscle have to operate over a longer trajectory,



3

Figure 3. Displacements of seven anatomical points relative to adult *H. elegans* as a result of the iterative perturbation procedure (filled symbols) and as found in *H. nigricans* (open symbols).

when the insertion of the tendon is closer to the corner of the mouth, than in the natural configuration. Given that the useful extension of muscle fibers depend on their resting length [7], the muscle fibers should be longer when the insertion of the tendon moves ventrad. The muscle fibers can become longer in three ways:

1. Extension of the fibers in caudal direction, which means that the origin of the muscle should move more caudally, which either results in elongation of the head, influencing functions such as respiration, hydrodynamic resistance, etc., or results in a decrease of opercular area, decreasing respiration capacity.
2. Extension of the fibers in rostral direction, which means that the tendon branch of the adductor muscle going to the lower jaw has to become shorter, decreasing maximum gape.
3. Omission of the aponeurotic sheet under the eye, which means that the eye has to become smaller, or heavily deformed, both resulting in a decrease in visual acuity and/or sensitivity [8].

This demonstrates that in *H. nigricans* a compromise between biting force on the one hand and gape, vision and respiration on the other hand is present in the construction of the jaw mechanism. It also explains the erroneous prediction of the position of the seventh anatomical point. In this way, perturbation analysis is a tool with which functional compromises in design can be indicated.

5. DISCUSSION

Changes in proportions of a complex functional component can be simulated mathematically, guided by an imposed change in a functional demand. The case of the jaw mechanism I described in this paper serves as a demonstration of the above thesis.

Lakatos [6] tells us that novel facts are indicative of a progressive research programme. Novel facts may be used to explain differences between prediction and observations when they are confronted. Such a novel fact was found by recognising the importance of the function of vision for the biting force transmission. However, it is not straightforward to use the function of vision for new calculations of optimal design in the jaw mechanism. There is no way that the functional demands of biting and vision can be weighed mathematically without being in the possession of a huge databank of ecological information. Knowledge should be gained on the relative importance of functions for the survival and reproductive success of the species.

Perhaps simulating evolutionary process by taking into account the most important functions of an organism in relation to the natural ecological conditions is the future of perturbation analysis. Presently, however, it seems more workable to analyse functions separately and finding novel facts there were functional components are forced into compromise.

It should be stressed here, that I dealt with a mathematical transformation from one species to another. This transformation is an analog of historical process. I did not say that *H. nigricans* actually evolved along the same pathway as the calculated version from an ancestor with the same proportions as *H. elegans*. However, if one wishes to transform one species into another with a minimum of morphometric change, and a given increase in biting force transmission, one should do it along the pathway described by the model analysis.[3]

The mathematical exercise shows us the morphometric consequences of improving a function. It shows numerically how functional demands can be in conflict because of limited space inside the organism. Especially for those who are interested in evolutionary process, it is instructive to see how a complex of morphometric changes are induced when one single function needs to change. "Hot spots" are uncovered by mathematical analysis, which focus attention on parts of the organism of high evolutionary importance. Only small changes in position of these points result in considerable changes in the function that is considered and if that particular function is decisive for it, in fitness.

6. APPENDIX

Perturbations of position of anatomical points

When a three-dimensional model exists of some mechanism of which the nodal points or anatomical points as recognisable in the apparatus are defined by their coordinates, some quantity indicative of the function of the mechanism can be changed by changing the positions of these anatomical points. The question is: in which direction do these points have to be moved in order to change the functional parameter with a minimum of change in position of the points and which points have to be moved first.

A mathematical technique has been devised to give an answer to this question. This technique will be outlined here:

1) Move each anatomical point sequentially, each along the three coordinate axes, over very small distances and calculate in every new situation the resulting value of the functional parameter which is under consideration.

2) By adding the effect vectors (the improvement of the functional parameter along the three coordinate axes), one obtains the direction in which the anatomical point should move. Calculate this direction for every point.

3) The magnitude of the sums of the effect vectors along the coordinate axes of every point differ and form an indication of the relative importance of the points for improving the functional parameter. A selection of a group of most important points leads to the identification of "hot spots". These are the points of which displacement quickly leads to change of the functional parameter. (Mathematical background: [9] .)

4) Select the point of which the displacement is most effective and displace this point in the optimal direction as calculated in 2). Now we have the starting configuration with only one point displaced. The functional parameter is improved.

5) Repeat the procedure, from 2) through 5), a number of times.

6) After a numer of trials, a few points will have been selected and displaced, leading to a change in the apparatus towards a more effective apparatus in terms of the functional parameter under consideration.

NOTES

1. A comparable line of reasoning, although not numerically proliferated, is given by Zweers [10].
2. When the procedure is repeated many times, the jaw mechanism comes to lie in the medial plane and the fish head becomes flat as a leaf, very much like the "leaffishes". The jaws become very short, resulting in a very small gape. The eyes reduce and the tendon of the adductor muscle of the upper jaw connects almost in the corner of the mouth on the maxilla close to the insertion of the maxillo-dentary ligament. As can be seen from this, good vision and large gape are reduced because of the improved biting force.
3. A similar process was outlined by Dullemeijer [3] when transforming four genera of snakes into each other by focusing on the presence of the pit organ.

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JAW PROTRUSION, AN OPTIMIZATION OF THE FEEDING APPARATUS OF TELEOSTS?

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ABSTRACT

A comparison of nineteen taxa of teleost fishes suggests the gradual acquisition of systems of upper jaw protrusion in the course of fish evolution. However, in view of the loss of protrusion in several groups of advanced teleosts the biomechanics of protrusile jaws are analysed based on the hydrodynamics of suction feeding. Calculations show that protrusion may reduce the energy otherwise spent in a feeding act to get the predator's mouth as near to the prey in the same time with about 80%. Other generalized advantages and disadvantages of upper jaw protrusion are explained. Detailed ecological data to calculate the balance between pros and cons of jaw protrusion of a particular species in its habitat are still lacking. There is no incompatibility between presence and disappearance of protrusile jaws in fish and current neo-darwinistic theories of evolution.

1. INTRODUCTION

As part of the symposium on Evolutionary Morphology of the Actinopterygian Fishes Rosen [25] discussed the popular notion that "acanthopterygian fishes (the atheriniforms and percomorphs) represent a sort of pinnacle of teleostean fishes". Gosline [5:5] states that some 50 families of basal percoid fishes represent the greatest focal point of fish evolution" and "dominate all of the richer marine faunas". These fishes are thought to be superior with regard to "manoeuvrability and diversity of feeding adaptations associated with the protrusile mouth". Rosen rejects this view.

Systematic research based on empirical studies of morphology, physiology, mechanical integration and behaviour leads to the construction of a branching diagram expressing the relationships between teleost groups. To investigate whether a certain progressive development of characters is present related with locomotor and feeding mechanisms four characters were

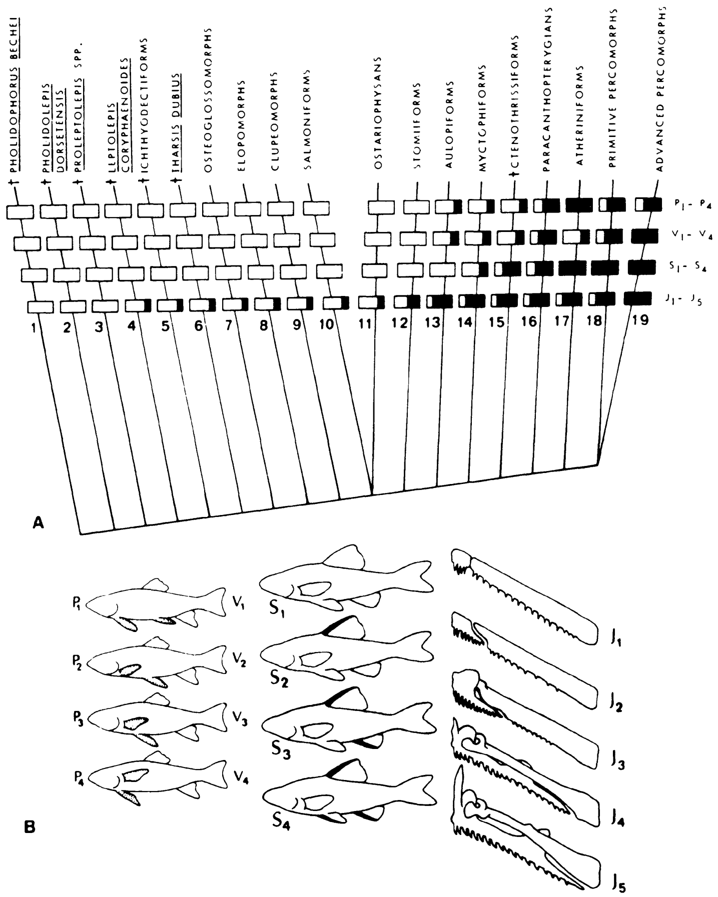

fig.1 B

Figure 1. A graphic representation of the presence of four characters in four or five character states in a cladogram of teleostean interrelationships. P_1-P_4 pectoral fins, V_1-V_4 ventral fins, S_1-S_4 fin spines, J_1-J_5 associations of premaxilla and maxilla. a) distribution of the characters, b) schematic drawing of character states. From Rosen [25], with permission.

selected, each of them split in four or five character states. Rosen [25] used the position of the pectoral fins, the pelvic fins, the presence of fin spines and the association of maxilla and premaxilla. Transformations of these four characters in nineteen groups or species of teleosts, six of them being fossil, are combined in a character-state tree of pectoral and pelvic fin positions, fin spine occurrences and upper jaw types. The character state of the most primitve member of a lineage is given. The result (fig. 1) suggests a seemingly regular pattern of character transformation of the different locomotor and the different feeding mechanisms. A historical interpretation is that changes in jaw mechanics arose first in teleosts with a still primitive arrangement and morphology of the fins. In later groups the pectorals and pelvics shifted position to a respectively more dorsal and more anterior position and fin spines gradually developed. Apparently a theory about the evolution of protrusile upper jaws does not require a concomittant theory about a correlated change in fin position or morphology. So far this analysis although at a rather superficial level as the author calls it himself, does not evoke counting arguments.

Rosen, however, proceeds by stating that these transformations cannot be proven to lead to adaptively superior fishes: "The idea that inevitably evolution results in functionally better systems is simply a derivative of the human reasoning for causing transformations" (p.271). A strong contrast is suggested between "the empirical studies of systematics" and the lack of proof in the assertions of some functional morphologists. The explanations in the evolutionism of some functional anatomists is only constrained by "their own inventiveness... and the gullibility of their audience".

In the following I will discuss only a limited problem viz: Is protrusility of the upper jaw an improvement of the constructions used for obtaining food? Does it increase the chance of catching a prey or reduce the energy spent in feeding activities? Having obtained an answer to this I will shortly proceed to other questions posed by Rosen [25] *e.g.* do reverse morphological transformations, including loss of protrusible jaws within several groups of advanced teleosts prove that a functional and evolutionary interpretation of these changes is impossible? Finally the point will be raised whether there is such a strong contrast between the "empirical studies of systematists and "the inventiveness" of functional morphologists.

To answer the question of the biological significance of protrusion I will use the hydrodynamical model studies on suction feeding in fish [10, 11,18,19,20,22] . These studies were performed to analyse the invariant constraints on fish feeding set by the physical properties of water and formulated in hydrodynamic laws. The options of feeding fish to optimize the mouth size, the amount of sucked water, the velocity of the water, the initial prey distance are described in these papers, providing a framework of possibilities. Why some fishes have chosen for a predatory and others for a filtering, scraping, biting or other lifestyle is a question related to the opportunities in a particular habitat, the other occupants of the niche and historical factors.

2. PROTRUSILE JAWS

Protrusile upper jaws are characteristic features of most acanthopterygian fishes. Such jaws are also found in the Cyprinidae belonging to the Ostariophysi [1]. The morphological and kinematical details of jaw protrusion appear to be quite variable. Liem [13] describes four different ways to accomplish jaw protrusion in cichlids only. Motta [17] reviews the literature on jaw protrusion and mentions four coupling systems producing protrusion viz: 1) lower jaw depression involving ventral movement of the distal part of the maxillary causing rotation of the maxillary head, 2) screwlike twisting movement of the maxilla, 3) neurocranial elevation, single or combined with lower jaw depression and 4) protrusion due to suspensorial abduction whether or not combined with lower jaw depression or cranial elevation. Experimental evidence concerning the components of the input movements essential to bring about protrusion is very scarce which is due to the complex systems of ligaments between the proximal parts of maxilla, premaxilla, rostral cartilage, palatine and ethmoid, often interconnected by folded skin sheets. The system is altered in unpredictable ways by severing one or several ligaments thus preventing straight forward conclusions on the necessary input movements or the required size of the forces.

A far better way to study the mechanism of protrusion is the construction of a mathematical model of the jaw apparatus, supported by a two-dimensional kinematic model. Otten [23] showed that neither the axial rotation of the maxilla (as suggested by Alexander [2] for generalized percoids) is a prerequisite for protrusion in *Haplochromis*, nor the squeezing action of the palato-palatine ligament as suggested by Liem [14]. Protrusion in this fish results from the combination of the following forces: the distal part of the maxilla pushes the distal tip of the dentigerous arm of the premaxilla rostrad and the intermaxillary ligament pulls its ascending limb ventrocaudally, the rostral cartilage is hereby pushed against the vomerine ridge and a protruding force on the premaxilla results (Otten's fig.4,p.70).

Functions of jaw protrusion are described by Schaeffer and Rosen [26], Alexander [2], Liem [12], Osse [21], Gosline [6], Muller and Osse [18,20], Lauder [9], van Leeuwen and Muller [11]. They have been summarized by Motta [17]. The listed functions include:

- momentarily increase in the rate of approach of the predator to the prey;
- increase of the initial distance from which a prey may be sucked;
- decrease of lower jaw rotation required to close the mouth once a prey is captured.

Several more functions are mentioned and others are considered to be possible in specific circumstances *e.g.* protrusion allows food to be obtained from otherwise inaccessible locations; protrusion allows a distance between the feeding fish and a possible harmful substrate (*e.g.* coral tissue with nematocysts), it allows a sharp angle between body axis and substrate during bottom feeding due to a ventrally protruded mouth. This facilitates a rapid escape from a predator because of the so reduced inclination of the body axis with respect to the substrate. The increase in distance might also widen the field of vision of the feeding fish [17]. The importance of protrusion is also suggested by the fact that *Haplochromis elegans* larvae with a head width of 1 mm already have functional jaw protrusion at their first free swimming stage after mouth breeding [23].

3. HYDRODYNAMICS OF FEEDING AND JAW PROTRUSION

3.1. General aspects

Feeding involves the approach to the food, but in the aquatic habitat this movement causes not only caudal and lateral, but also rostral movement of water. This result of the pressure exerted on the tip of the snout [22] of the approaching predator causes a force on a free-movable food object tending to push the prey forward. Since this force and the resulting movement increase with diminishing distance between the fish and its food the pressure point on the snout tip should somehow be removed. This is done by opening of the mouth during the approach. Now the speed of the fish will be slowed down considerably, unless the expanding buccal and or opercular cavity can take up the water entering through the mouth. If the volume increase of the expanding cavities just compensates for the water entering the mouth as a result of forward motion through swimming, no acceleration of the inward flow occurs. The water in front of the moving mouth remains stationary with respect to the moving fish. When the mouth expansion exceeds this speed a suction flow to the mouth will develop thus increasing the chances to procure the food. When during this action the position of the mouth opening moves towards the food through protrusion of the premaxilla a further increase of the capture chance occurs.

A hydrodynamic model of the system used for suction feeding was constructed [19] enabling the calculation of instantaneous velocities and accelerations of the ingested water and prey. Input parameters in this model are timing and extent of head movements, fish head dimensions and swimming velocity.

3.2. Quantitative effects

From the hydrodynamic model of Muller and Osse [18,20] Van Leeuwen and Muller [11] derived the following formula for the relative prey velocity, *i.e.* the velocity of the prey with respect to the mouth opening of the moving fish:

$$U_{prey} = U_m e_{su} + U_{mp} e_{su} + U_{sw} e_{sw} - U_p \quad \text{(eq.1)}$$

(U = velocity m/sec, e_{su} = suction effect, e_{sw} = swimming effect, m = mouth, p = protrusion).

U_{prey} is the relative prey velocity, $U_m e_{su}$ is the contribution to relative prey velocity due to suction if no protrusion would be present, $U_{mp} e_{su}$ the contribution of protrusion to suction velocity due to increased head length, $U_{sw} e_{su}$ is the contribution of swimming to the relative prey velocity and U_p is the contribution of the translation velocity of the mouth opening through protrusion to the relative prey velocity.

The forward velocity of the fish is taken to be positive, velocities directed towards it, negative. The parameters $e_{suction}$ and $e_{swimming}$ are functions of mouth radius and the distance between prey and predator (*cf.* Van Leeuwen and Muller [11] p.147 for details), they symbolize the effect of suction and the effect of swimming. The velocity of the prey was expressed in a system of coordinates fixed to the moving mouth aperture rather than in an earth bound frame because the former is the important parameter in prey capture.

Fig. 2 shows the calculated effects (equation 1) of swimming (line 1), the effect of protrusion added to 1 (line 2), the effect of suction plus

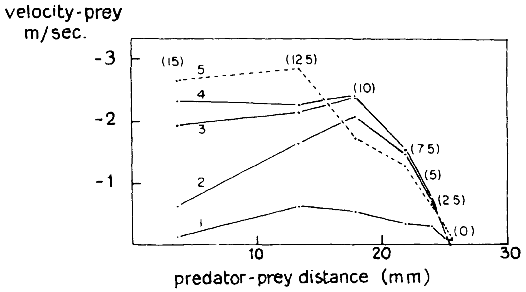

fig.2

Figure 2. The contributions of swimming, protrusion, suction and the suction effect of protrusion to the velocity of the prey in a feeding act of *Pterois* calculated from eq.1. The dashed line indicates the velocity of the prey measured from frames of 400 fr/sec movie. 1 = swimming, 2 = swimming with protrusion; 3 the sum of swimming, protrusion and suction, 4 as 3 with the addition of the increased suction effect due to protrusion 5, velocity measured in experiment. From Van Leeuwen and Muller [11] with permission.

1 and 2 (line 3) and the summed effects of all four terms to the velocity of the prey seen in the moving frame of the predator's mouth (line 4, [11]. Line 5 depicts the velocity as measured from the frames of a 16 mm film. Also the other data used for the calculations were derived from a movie of a feeding *Pterois* (lionfish). The good correspondence between the lines 4 and 5 strongly suggest that the graph can be used to judge the separate contributions to prey velocity of respectively swimming, protrusion, suction and suction with enlarged mouth length due to protrusion. Protrusion occurs early and then greatly contributes to prey velocity, later the increased suction effect compensates for the decreased contribution of protrusion. Note that the prey passes the mouth opening when it has its maximum velocity. From these data a rough quantitative estimation can be made of the energy saved by protrusion. A disadvantage of using the velocity data of Fig. 2 for the calculation of energy is that the distance between prey and predator in the moving frame is changed by movements of both. As we are interested in the contributions of different movements of the predator the original data from measurements in the earth bound frame were used.

The total distance covered by the mouth opening of a feeding lion fish (*Pterois russeli*) in the example of Fig. 2 is 23.1 mm, 10.1 mm contributed by swimming and 12.6 mm by protrusion of the upper jaw (measurements in five successive frames of 400 frames/sec. movie). As the mass (0.06 kg) and the length (142 mm S.L.) are known energy calculation can be made.

As neither the mass of the moved water nor the velocity given to these masses is known the approximation is made that the energy lost to the moving water is equal to the energy spent in moving the fish as a whole or moving its upper jaws.

When no protrusion would occur and the lowest acceleration is used to cover the above distance with the mouth opening in 15 m sec the feeding action would cost 0.57 J. In fact the fish as a whole only covers 10.7 mm which costs about 0.12 J. As the mass of the premaxilla and the adjoining parts is less than 1% of the body weight the energy necessary to obtain the maximally measured protrusion velocity of 1.6 m/sec is only 0.003 J. So taking into account only this aspect of protrusion and omitting above mentioned other possible advantages four-fifth (about 80%) of the energy otherwise necessary to get the mouth opening in the same time span at the same spot is saved. Calculations using the Fig. 2 velocity data also show an energy saving of 80%. In these calculations no allowance is made for the energy necessary to overcome drag. Because of the small wetted area of the protruding mouth tube as compared to the surface of the body as a whole the inclusion of drag would only demonstrate a higher energy saving for the power required to swim a given distance in a given time is proportional to the third power of the velocity.

So the hypothesis that protrusible jaws as an energy saving device are highly advantageous, is confirmed. Its savings rise when many feeding acts per unit time are necessary as *e.g.* in fish larvae. The early acquisition of a functional protrusion system in *Haplochromis* [23] as well as in *Cyprinus* are in agreement with this prediction. Also for other fishes, a flounder (*Platichthys*) and a pike perch (*Stizostedion*), the contribution of the four terms in the formula to the velocity of water and prey was calculated and compared with experimental data. Protrusion does not occur in *Stizostedion*, the relative prey velocity is made up of swimming later supported by suction, the terms number three and one in equation 1. In the flounder especially the translation effect of protrusion contributes to the prey velocity, its relatively small effect on suction due to the increased head length gained by protrusion is not fully utilized because protrusion is still going on when the prey passes the mouth opening (I. Oomen, unpublished data). So the quantitative reduction of energy expenditure due to protrusion in the capture of a prey can be estimated. The contribution of protrusion in reducing the initial prey distance amounts to about 50% in feeding acts of the lion fish. Rotation of the maxilla closes off the angles of the mouth, so the intake of water lateral to the predator's head not containing the prey, is prevented.

Besides, calculations and observations by Muller and Osse [20] show that the increased velocity in the horizontal direction due to protrusion narrows the angle of the funnel of ingested water in front of the mouth. So protrusion in combination with forward motion and suction enables the fish to select the form of the volume of water to be ingested (*cf.* [10]).

Here we abandon for a while the strictly biomechanical view of protrusion and pay attention to its regulating system. The volume and form of the watermass to be sucked during feeding depends upon the following parameters: mouth radius, timing of mouth opening during the approach to the prey, timing of start of protrusion, velocity and distance of protrusion, instantaneous swimming velocity and the amount and timing of the expansion of buccal and opercular cavities. Let us consider some extremes. Hardly any forward motion of the predator combined with fast protrusion, considerable protrusion distance and appreciable suction would mean a flow of water from a wide angle into the mouth with high velocity, suitable to obtain a fast starting prey item, because even when the prey has moved from its original position it will still be contained in the volume of sucked water. Fast forward swimming with hardly protrusion, late mouth opening and expansion would be a proper strategy to obtain a fast prey with a good predictable position at the moment of capture. In Muller and Osse [20] more detailed data are presented, the above suffices to show that the regulation of timing and amount of movements during feeding, together with a protrusion device, increase the versatility of the feeding apparatus, strongly suggesting that a greater diversity of food items can be captured successfully. The neuro-muscular control system must keep up with the increased morphological complexity.

Recently Sibbing [27] showed that in cyprinids also after food up-take protrusion is important, contributing to the selection between food and non-food material contained in the oro-buccal cavity. The protruded upper jaws with the mandibles and the stretched area of skin form an additional anterior volume of the oral cavity, closed off from the environment. It is used to contain water during selection, a process of forth and back flow of water with suspended particles between buccal and opercular cavity propelled by movements of mouth bottom and fill covers. This enables the fish to separate useful from waste material with its branchial filter and palatal organ. This exemplifies the unexpected functional importance of a character hitherto mostly associated with food uptake only and not with food handling.

The apparent complexity of the functional relations of the protrusion system strongly suggest that the problem of the functional advantages and disadvantages of such a system of jaws in its evolutionary development easily leads to false generalizations.

4. COMPLICATIONS OF PROTRUSION DURING BITING

The improvements of protrusion during suction feeding mentioned above do not apply when the same apparatus is used for biting. The transmission of biting forces applied to the premaxillary onto the skull is endangered by its rather fragile suspension to the ethmoid region. The strong palatine protuberance that extends forward over the anterior head of the maxilla in most acanthopterygians is supposed to be a key element in the system supporting the protruded jaws [7] . Otten [23] showed that the A1 part of the jaw adductor muscle can stabilize the protruded upper jaw during biting. Motta [16] showed that *Chaetodon miliaris*, a butterfly fish, shows protrusion in the majority of suction bites but also feeding without jaw protrusion occurs depending on the nature and position of the prey. Biting with protruded jaws was also described in other teleost species, *Gasterosteus* [3] , *Crenilabrus* [8] and *Haplochromis* [4] . No data are available to correlate the relative frequency of biting, suction or combined feeding action with the presence of a protrusile jaw apparatus. The absence of protrusion in some otherwise typical acanthopterygians strongly suggests the hypothesis that in these fishes powerful biting is predominant during feeding.

Protrusion, leading to the rapid formation of a round hydrodynamically optimized anterior mouth opening for suction feeding also reduces the length of the toothed jaw edge to grasp, retain or bite a prey. At present the multiple objectives of the jaw apparatus of fish cannot be compared in their separate contribution to survival. This implies that a particular construction of the jaw apparatus may be the result of a compromise between incompatible functional demands. This again is strongly suggested by the perturbation analysis of Otten [23] . The change of six proportions alters *H. elegans* into *H. nigricans* with a threefold increase in biting force but with a reduced mouth size.

5. DISCUSSION

According to Rosen the advantage of functional morphological studies is that "the nature of organic diversity can become known in detail" increasing our character discrimination. The rejection by this author of the idea that "evolution inevitably results in functionally better systems" is understandable because the notion "better" cannot be used in this indetermined sense. "Better" with respect to what? How to judge "better" in an objective sense?

The details about protrusion amply show that such a set of structural tools has quantifiable effects on the energy spent during feeding and also on the chances to catch a food item. In every species, at different times in the life cycle, in situations differing in light, turbidity, different also in type, size, position and escape possibilities of the food the possession of a protrusable jaw system will differ in its balance of beneficial and adverse effects. So "better" must be judged not for a group, but for a particular fish in particular conditions. These data averaged over the lifespan of the fish and the probabilities of encountering certain food types in a particular set of abiotic conditions would allow the objective decision whether a certain morphological trait adds to survival and reproduction.

Fitting in this approach is also the common observation of the existence of functional alternatives and multiple use of structures. This applies as we have seen not only to the "all or none" use of a construction in a given environmental situation but also to the degree and timing of its application, so in a qualitative as well as a quantitative sense. Evolution seen as a continuous change in organisms and environment presupposes a variable difference between what would be optimal in a particular set of conditions and the actual situation encountered in the individual. So protrusile jaws can be still found in species changing their food-choice to increased biting as possibly in *Chaetodon* [16]. The intermediate character states of the association between premaxilla and maxilla as found in Aulopiforms (fig.1b, p.4) with a non-protrusile premaxilla but a rotating maxilla might be considered as a functional system suitable for biting combined with suction [24]. The maxilla will close off the angles of the mouth, during suction, the increased number of branchiostegal rays will aid in caudal volume increase, suction, with closed opecular valves. In view of the disadvantages of protrusion the reverse transformation of the jaw condition in many taxa is no empirical constraint to a "general functional and evolutionary interpretation of these morphological systems" [25:269]. On the contrary, these facts show that knowledge of functional morphology is a prerequisite to study the relations between animals in a taxon, because it shows that seemingly separate characters are functionally tied into constructions for particular roles. As every character of a fish is an ecological character knowledge of the biological relevance of structures will help to bridge the gap between students of living and of dead animals.

Percomorph fishes are not a pinnacle of fish evolution but apparently they are often able to drain off a considerable amount of the energy present in many ecosystems under present day environmental conditions. The same is true for computer engineers as compared to farmers in the human society, even although the former have hardly relationships with primary production. The abundance of herring in suitable environments amply show the functional potentialities of ancient construction types.

The rejection by Rosen of what I would call "Little Red Riding-hood" functional morphology *i.e.* suggesting functions for structures and then concluding to their adaptive significance has my strong support. However if structural and functional studies are followed by the construction of a model providing falsifiable hypotheses to be tested in nature (*cf.* [28]) functional morphology is a powerful tool to analyse supposed adaptations of structure. Such models are also quite useful to test the adaptive significance of alternative structural solutions found in related types.

The loss of protrusile jaws in some taxa of acanthopterygian fishes suggests a niche-shift of these groups. Magnan and Fitzgerald [15] have shown that niche-shifts can occur as a result of suddenly sympatric fish species, as distantly related as creek chubs and brook charr. Apparently processes supposed to occur in a Darwinian theory of evolution do exist. We have no way to determine the importance of such processes in past events in the course of fish evolution. The biomechanical analysis of advantages and disadvantages of protrusion as well as the ecological data showing niche-shifts in sympatric fish show that the appearance and disappearance of protrusion within taxa of teleosts is entirely compatible with current evolutionary theory.

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CONSTRUCTIONAL MORPHOLOGY: THE ANALYSIS OF CONSTRAINTS IN EVOLUTION

DEDICATED TO A. SEILACHER IN HONOUR OF HIS 60. BIRTHDAY

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ABSTRACT

Evolutionary change is opportunistic, but its course is strongly constrained in several fundamental ways. These constraints (historical/phylogenetic, functional/adaptive, constructional/morphogenetic) and their dynamic relationships are discussed here and shown to constitute the conceptual framework of Constructional Morphology. Notwithstanding recent published opinions which claim that the "discovery" of constraints renders Neodarwinian selection theory obsolete, we regard the insights of Constructional Morphology as being entirely consistent with this theory. As is shown here in the case of the *Hyracoidea*, formal analysis of the constraints which have framed the evolution of various characters extends our understanding of the evolution of a taxon.

1. INTRODUCTION

The term "constructional morphology" has been used with several different but related meanings which have collectively given rise to considerable ambiguity. The purpose of the present paper is to clarify these different meanings of the term and to outline an analytical approach to the study of the origins and evolution of organic form that has been designated as "Constructional Morphology". This particular approach was first suggested by Seilacher [56] and has been developed further by Reif [43,45,46] , Thomas [62] and Thomas and Reif [63,and in preparation] . (A similar concept, with a different name, was already developed by Van der Klaauw [25,26,27] and Dullemeijer [11,12] .)

1) Some have employed the term constructional morphology to emphasize the functional and architectural integration of organic structures, as analogues of machines (see Reif, in press, for a review). Bock and

v. Wahlert [3] and Peters *et al.* [38] have indicated complementary ways in which organic form may be explained within the framework of evolutionary biology. One analyses the biological role of an organ by testing possible answers to the question: "What is the utility of the organ?" This search for adaptation is the province of functional morphology, as this field is usually conceived. Alternatively, one seeks answers to the question: "How does the organ work or operate?" This question seeks to understand the design, the physical and chemical processes, and the action of the organ. The attempt to answer this latter question has been called constructional morphology. It represents the morphological aspect of biophysics and physiology. Whereas modern experimental biophysics and physiology are largely reductionistic, constructional morphology focuses on higher levels of integration [38] . This concept of constructional morphology is independent of the postulate of evolutionary change. It has a long history (Reif, [47] extending back at least to the work of Cuvier and Geoffroy, Russell [53]). It is noteworthy that a very broad research program was developed in the 1870s, and that direct comparisons between organs and technological inventions have long been a standard method. The application of this sort of analysis in paleontology was long neglected but Böker [4] and D. v. Kripp [28] seem to have been pioneers of its revival in this century.

2) The entomologist Hermann Weber chose the term "Konstructionsmorphologie" for a new approach to morphology. After WWII he developed a research program that was only incompletely worked out and published due to his early death [67,68,8] . The fullest account is given in unpublished notes distributed at a lecture series [48] . Weber's goal was to provide a new methodological basis for morphology, so that the necessarily descriptive science of morphology could compete with the more fashionable areas of experimental biology. Weber rejected evolution (*i.e.* the theory of descent) as an axiom of morphology, because he wanted to avoid the naive speculative phylogenetics which, according to him, had plagued morphology since the time of Haeckel. Also Van der Klaauw [26,27] took this position and he simultaneously introduced a holistic approach, which had a strong influence on his students (see [13,14] for reviews). The only sound basis for a method which Weber found was typology, which he tried to free of all its metaphysical connotations. The first step in Weber's method is to provide an exact, empirical description of the taxon.

Building on this objective basis, causal determinants of form are incorporated step by step. First one analyses morphogenesis, ontogeny and the alternation of generations. Then one develops a plan of construction which incorporates function, mechanical operation and the change of form and function during ontogeny. Weber did not distinguish between the function and the biological role of a character, so it is not clear how ecological data could be incorporated into this functional analysis.

The analysis proceeds from an ontogenetic time-scale (development) to the evolutionary time-scale (relationships among taxa). This is accomplished not by deduction from the theory of descent but by induction (analysis of morphological similarities). The fact of evolution (Theory of Descent), phylogenetics (Reconstruction of Relationships), and causal factors of evolution (Theory of Selection, Theory of Speciation) are not clearly distinguished in Weber's writings. This explains in part Weber's reservations about what he called "evolutionary methods". It is obvious that Weber did not seek to contribute to the causal explanation of evolution, nor did he want to develop an "evolutionary scenario" (*i.e.* an integrated account of the phylogeny and evolutionary ecology of a taxon). His goal was to provide a non-speculative description of the phylogeny of a group of taxa. Consequently, the next step is to arrange the analyzed types in an hierarchical order. This pattern leads to the recognition of a "Prototypus", from which "all other forms" can be derived. The prototype is then interpreted in phylogenetic terms as the "paleotype". Now the fact of evolution is accepted and the ideal connections between the types are reinterpreted as genealogical relationships. Progress beyond this "evolutionary tree of types" is only possible if paleontology provides appropriate data. If the prototype can be equated with a real fossil taxon, it becomes the "ancestral form". The last step is to describe the phylogenetic history of the diversity of the group.

3) The paleontologist A. Seilacher, who had attended Weber's lectures, introduced the term "Konstruktionsmorphologie" as the title of yet another research program [56]. His basic premise was that a functional interpretation was a necessary but not a sufficient explanation of organic form. Organic form could be understood only if it was seen as the result of the operation of three factors: adaptation, phylogenetic history, and "Bautechnik" (principles of morphogenetic fabrication). Seilacher's Bautechnik-aspect introduces a significant component that is independent of the action

of natural selection. It recognizes the laws of geometry, natural materials, and growth processes give rise to patterns that are in some cases "non-adaptive", like certain colour patterns in molluscan shells. Seilacher's goal was to go beyond traditional functional and constructional morphology, to provide a more complete and flexible framework for the analysis of organic form, recognizing the roles of independent factors and incorporating dynamic processes of individual development and evolutionary change. For a similar concept of the "Leiden school" see Dullemeijer ([14] , with many references) and Zweers (this volume).

2. ORGANIC FORM, EVOLUTION AND CONSTRAINTS

We have further developed Seilacher's concept and the present account in part summarizes a longer paper in progress. Two questions which complement one another lie at the core of our conceptual framework: (1) "What absolute constraints, if any, limit the range of possible organic forms?" and (2) "How is the course of evolutionary change constrained by the nature of its processes and their action in *this* world?" Our inquiries, provoked by these questions, lead to the recognition of a set of constraints on form, which can be classified in different categories. These constraints help to explain a variety of evolutionary phenomena, such as suboptimal structures, convergence, parallel evolution, chanelled evolutionary pathways, and the geometrical patterns that characterize organic structure.

This approach to the explanation of form is in full accord with the Synthetic Theory of Evolution. In no way does it contradict the theory of evolution by natural selection, broadly construed. We view this approach as a natural extension of modern evolutionary theory. It integrates functional and constructional morphology (in their classic senses) with ecology in an explicit evolutionary context.

When Seilacher [56] first published his essay, the role of constraints in evolution was accorded little interest. Authors like Waddington [66] , Weiss [70] and Olson [37] who challenged the then dominant (pan-) selectionist view were regarded as mavericks in the community of evolutionary biologists. The adaptationist view of that time is well exemplified by the work of Cain [7] . Mayr [33,p.2] listed "mutational limitations" and "epigenetic limitations" in a table of evolutionary factors that had been proposed by earlier authors, but these topics received no further comment here and little elsewhere in the book. One of the first to draw attention to "nonadaptive aspects of evolution" in the context of the NewDarwinian synthesis was Van Valen [64]. Recent textbooks (*e.g.* [10,22,29,30,60]) include no discussion of the roles of constraints on the process of evolution by natural selection. Rare exceptions are Salthe [55,p.315-328] in his chapter "The best of all possible worlds", and Futuyma, [16,p.386-387] who addresses "failures in adaptation" and related subjects. Only recently has the concept of constraint received much attention in various areas of evolutionary biology (functional morphology, developmental biology, ecology). Reacting to a provocative caricature by Gould & Lewontin [21] of attempts to explain form, behaviour and evolutionary change in terms of adaptation, Mayr [36] has defended the adaptationist program. He claimed that the notion of constraint is not in conflict with the synthetic theory and he listed five kinds of constraints (*cf.* [1,5,14,41,43,56,62]; see also Mayr, [34]):

1. A capacity for nongenetic modification (ecophenotypic response).
2. Multiple evolutionary pathways. The adoption of a particular solution may greatly restrict the possiblities for subsequent change.
3. Stochastic processes.
4. The target of selection is always the individual as a whole, rather than a single gene or an atomized trait.
5. Cohesion of the genotype.

The flurry of recent interest in constraints is also reflected in Mayo [32] "Natural Selection and Its Constraints".

3. A NEW THEORY OF EVOLUTION?

Philosophers of science have long tended to see all scientific enterprise in the light of physics. However, it is now becoming clear that physics cannot be regarded as *the* model science. Historical sciences like biology and geology differ significantly from physics ([57]; see discussion in [35]). Nevertheless, controversy continues among biologists and philosophers of science over the nature and utility of theories in natural history, especially over evolutionary theory, which incorporates numerous subsidiary theories and hypotheses.

Over the past few years, the synthetic theory has repeatedly been declared "effectively dead" [19], "on the verge of crumbling" [20], "insufficient" [24], as no longer acceptable (see [6,51]), or as an "altdarwinistisches Dogma" [23]. Recently Webster & Goodwin [69] have vigorously attacked the synthetic theory. "The organism as a real entity, existing in its own right, has virtually no place in contemporary biological theory" (p.16). "Genetic and environmental concepts exhaust the explanatory repertoire of the (neo-Darwinian) paradigm vis-a-vis form" (p.31). "We regard the theory of evolution, and in particular neo-Darwinism, as having extremely limited explanatory power with respect to the problem of form to which it was originally addressed. This limitation arises as a consequence of the absence of any adequate theory of the means of production of 'typical forms' and is such, we would maintain, as to render debatable the claim that neo-Darwinism is the unifying theory in biology" (p.44). Webster & Goodwin argued for a structuralist approach: "The general aim of structuralist theory is to make the order of a unified system intelligible. It aims to express a formal system in which 'the actual is explained or interpreted as an instance of the possible' [39]" (p.41). "A structuralist conception of living organisms with its emphasis on the logical, the universal and the necessary, implies that the organismic domain as a whole has a 'form', and is therefore intelligible (which does not mean predictable) and that the 'content' - the diversity of living forms, or at least their essential features - can be accounted for in terms of a relatively small number of generative rules of laws" (p.46).

We have quoted here extensively from Webster & Goodwin [69] for two reasons. First, the concept of these authors, who are developmental geneticists, parallels that which we developed in Reif [43], Reif and Robinson [50], and Thomas [62]. Second, however, we see this structuralist approach to the problem of form as being complementary to the synthetic theory and *not* as a contradiction of it. Ever since the time of Darwin [9] debate has continued over the content *and* status of the theory of evolution. The Darwinian theory in its various forms (neo-Darwinian; Modern Synthesis; recent Modern Synthesis, *sensu* Mayr, [33]) has been rejected by some authors for a number of reasons. Among these are: (1) the notion that the theory cannot be refuted or that it cannot be proven; (2) that it is incomplete; (3) that it produces wrong results; (4) that adherents of the theory neglect important aspects of organismic structure. Debate on the status of theories is a common phenomenon in natural history. Expansion of a theory may or may not involve refutation of the old theory and its replacement by a new one. We regard it as a virtue of the Darwinian Theory that it satisfactorily integrates the results of disparate modes of analysis. This does not mean that the theory is in any way vague or arbitrary.

Webster and Goodwin [69] see the structuralist approach as an alternative to both atomism and holism, which have dominated the history of biology. "Structuralism is concerned with order, its generation and transformation. It rejects both atomism and holism. Following Piaget [39], we may characterize it in terms of three key concepts: wholeness, transformation and self-regulation" [69:40]. Mayr [34:333] in his defense of the adaptionist program claimed: "A partially holistic approach (in other words, an adaptationist program which takes constraints into consideration) that asks appropriate questions about integrated components of the system needs to be neither stultifying nor agnostic. Such an approach may be able to avoid the Scylla and Charybdis of an extreme atomistic or an extreme holistic approach". These theoretical formulations differ in emphasis and terminology, but it is by no means clear that they prescribe different research programs. They differ fundamentally, however, in the positions taken in relation to the Synthetic Theory. This can mean either that acceptance or rejection of the theory is irrelevant (which most likely it is not) or that we still do not have satisfactory criteria by which the merits of such a theory can be objectively judged.

We see our own structuralist approach to the problem of form to be fully consistent with an evolutionary process in which selection is the sole *efficient* cause of change. Thomas and Reif [63] elaborate three categories of constraints: (1) historical/phylogenetic; (2) functional/adaptive; (3) constructional/morphogenetic. These will be discussed here. We do not regard this as a mere exercise in classification. On the contrary, a framework of constraints is necessary, because although the constraining factors may be treated as discrete variables, they are closely interrelated and complement one another. Many recent authors have emphasized the role of one or other of these factors, paying insufficient attention to their complex interactions.

4. HISTORICAL/PHYLOGENETIC CONSTRAINTS

The genome and epigenetic, developmental processes are highly buffered and stabilized systems. Minor disruptions are corrected by homeorhetic processes (*sensu* Waddington [65]); larger disruptions (on all levels) lead to a breakdown of the developmental process. Lethal mutations are only one example of such a breakdown. This stabilization of developmental processes (see Alberch [1] for a discussion) necessarily plays a strongly conservative role in evolution. Hence all organic forms have a strong historical component.

If we are to determine whether morphology evolves by small increments or in larger jumps, we must know how far the inhereted epigenetic "machinery" can be changed without a collapse. What consequences for adult structure follow from a given change in the epigenetic machinery? What kinds of changes are likely to occur; what are unlikely? Answers to these questions will come from the synthesis of genetics, epigenetics and evolutionary studies. There has long been an interest in the influence of developmental processes and timing on evolutionary change. In recent years this has led to several important publications, *e.g.* [5,18,40]. For the area of inquiry circumscribed by Raff & Kaufman's title: "Embryos, Genes and Evolution", Reif [49] has suggested the name: "Evolutionary Epigenetics".

Numerous phenomena of evolution can be largely explained by the conservatism of the inherited genome and epigenetic machinery, among them vestigial organs and atavisms, the constancy of Baupläne, and the stability of adult form within species. Striking instances of parallel evolution highlight the fact that potential adaptations are strongly predetermined by the genetic and epigenetic make-up of a taxonomic group [1].

5. FUNCTIONAL/ADAPTIVE CONSTRAINTS

The analysis of functional/adaptive constraints focuses on the interactions among parts of an organism and those between the organism and its environment. Every part of an organism has a biological role that requires some particular mechanical function. The variety of mechanically viable forms is limited *a priori*. However, the number of possible forms is further reduced by the condition that the parts must function in a given context, by which adaptive changes are constrained. The effect of these constraints varies, depending on a given situation. They may keep the number of multiple adaptive pathways [2] small; they may leave only one possibility open (*i.e.* they channel evolution); or they may prevent further change altogether. Convergence is usually understood as a result of adaptation in response to similar constraints. In this perspective, selection drives form towards a common optimal design, as in the eyes of vertebrates and squid, and the torpedo body-shapes of tuna, mako sharks and cetaceans. It is usually forgotten that other constraints play an important part in convergence. There may simply be only one possible solution to a given structural problem due to the laws of geometry, physics and chemistry (see below).

Concepts of optimal design, behaviour, or life history strategy have long served as models in ecology and evolution (see Stearns [58] for a review). Evolution by natural selection does not predict the achievement of optimal design. Organisms simply have to be "good enough" to survive. This means that they must be as good as or slightly better than their competitors. Nonetheless, we do find numerous examples where an observed trait is in close accord with an optimal model [59]. In other cases optimal models fail. In such cases a "satisfying model" applies, in which "the search for an optimum is replaced by the search for a stopping rule, for a way to tell when a good-enough alternative has been found" [58:13]. This means that students of adaptation should not only devise optimal models but have to learn to develop models which are "good enough" in a given situation, *i.e.* in a construction, in an ecological situation *etc.*

Optimal designs set standards for comparison in an important research strategy applied in palaeontology, the paradigm method of Rudwick [52]. In order to determine the function of a fossil organ, one constructs models that would perform alternative possible functions optimally. The function with the paradigm that is approached most closely by the actual structure is inferred to be most probable. Such a method should only be applied if one also takes other constraints into account. Concisely, optimal models constrained by historical and morphogenetic factors lead to satisfying models. Satisfying models are not alternatives to optimal models but are rather more sophisticated modifications of them. The problem remains that it may be rather simple to design an optimal model but it is often very difficult to discover the appropriate constraints.

6. CONSTRUCTIONAL/MORPHOGENETIC CONSTRAINTS

Historical/phylogenetic and functional/adaptive constraints act in a given context and they hardly ever set absolute, inescapable limits to evolutionary change. This is not the case for constructional/morphogenetic constraints, which are ahistorical and express limits placed by the laws of physics, chemistry, cybernetics and geometry on evolutionary change.

It may be argued that geometry and cybernetics are abstract mathematical fields, that what is here subsumed under "geometry" and "cybernetics" belongs to physics. Nevertheless we will speak of geometric and cybernetic laws here. The ahistorical constraints can be grouped into three categories:

a) The physical and chemical properties of available materials (elements, chemical compounds). Size limitations placed by physical laws on structures of all levels (cell sizes, sizes of locomotory structures, *etc.*). Size dependent phenomena such as adhesion, viscosity, and inertia (see Table 2 of Koehl, in [5:223]).

b) The number of possible growth programs for organic structures is limited. Each program yields a limited range of different solutions. This aspect has been designated as Theoretical Morphology (*sensu* [42] ; see [44] for references).

c) Cybernetic laws control development, homeorhetic processes, maintenance, and repair of the organism. We are far from having a clear understanding of these laws.

Acquisition of particular materials, growth programs and regulatory systems in the course of evolution constitute historical events, which subsequently result in historical/phylogenetic constraint. This historical aspect should not be confused with the clearly ahistorical aspect, inherent in the properties of the original materials, growth programs, and regulatory systems.

Convergence is often not the result of a common functional, adaptive constraint ("the optimal solution"), but may rather result from common constructional/morphogenetic constraints ("the only possible solution"). Analogous growth programs give rise to similar structures in very different taxa [50] .

In a recent paper on the relation between ontogenesis and patterns of evolutionary change, Alberch [1] has argued "that developmental constraints and interactions impose severe limits on the action of directional selection and can set up phyletic trends" (p.664), Alberch's examples involve the interaction of several different factors. Functional/adaptive, historical/phylogenetic, and constructional/morphogenetic constraints all operate on developmental pathways. A non-random change (*sense* Alberch) on an inherited developmental pathway is directed by (1) the inherited genetic and epigenetic machinery, which by historical accident happens to have properties such that it can be changed only in certain ways, or (2) by the functional integration of the inherited epigenetic pathway with other processes, or (3) by the cybernetic properties of the epigenetic processes themselves, whose law-like structure limits the range of future changes.

7. A SYNTHETIC VIEW OF CONSTRAINTS

The relative roles of the various determinants of form are most easily established for what we call "*Comparative examples*", where structures of different taxa are compared. Parallel evolution of structures that have evolved independently in closely related taxa clearly expresses historical/phylogenetic constraint. As shown above, convergence may express either evolution towards an optimal design, if it is determined by functional/adaptive constraint, or it may express the only possible solution to a structural problem and thus reflect constructional/morphogenetic constraint.

"*Non-comparative examples*" have to be studied individually because no appropriate comparisons are possible. Here, it is much more difficult to evaluate the relative importance of the three types of constraint. In the morphological (and ethological) perspective developed here, all evolutionary changes, however they are initiated, ultimately involve changes of function in response to a new adaptive situation, involving environmental change, exploitation of a key innovation, or selection towards optimality, for instance.

The first question asked is: "What structure, including its developmental pathway, is inherited?" As a second step, one seeks to establish the "past adaptation", the adaptive significance of the structure before its change of function. In the third step, one analyses the demands that are placed on the structure by its new function (*sensu* [13]). If these functional requirements are relatively unspecific and if the developmental pathway is strongly canalized, a change of function requires only minor changes in structure, in which case historical/phylogenetic constraints dominate (Solution no. 1). If the functional requirements are strong and specific, a change of function can be brought about only if the historical/phylogenetic constraints are relatively weak. The modification of structure which results is either controlled by functional/adaptive constraints, in which case it evolves towards an optimal design (Solution no. 2), or by constructional/morphogenetic constraints, in which case a "good enough" structure will evolve (Solution no. 3). In this model, historical/phylogenetic legacies are regarded as past adaptations, modified at each step in evolution within limits set by the three types of constraint. The three solutions are never absolute determinants of form. In each individual case, a compromise develops among the influences of the three factors.

8. CONSTRAINTS IN THE EVOLUTION OF HYRAXES

Hyrax evolution illustrates the effects of several kinds of constraint. Living hyraxes are rabbit-sized, plantigrade herbivores with very good climbing capabilities. They live in protected environments such as tree-crowns in the tropical rain-forest and caves within rocky mounds of the African savanna. Hyraxes are thought to have evolved from three-toed, digitigrade steppe-runners [15,61].

Historical/phylogenetic limitations are shown in cases where morphological (or behavioural) characters are not immediately related to the current ecology of a group. Such discordance may be indicated by comparison between the character of the group under study and equivalent characters of ecologically similar taxa. Hyraxes have a gestation time of 7-8 months. Neonates are fully developed: they can see and are active on the first day and start feeding on the third day after birth; three premolars are already erupted at birth and the fourth starts to erupt; and litter size is small, *Dendrohyrax* having 1-2 offspring, *Procavia* and *Heterohyrax* having 2-3 offspring. These characters are usually found in mammals which live in open areas, like steppes. Groups living in caves (*e.g.* rodents) tend to be r-strategists, with large litter sizes and altricial young. This seeming contradiction suggests a significant ecological shift in the evolution of the hyraxes [4,17,54].

Functional/adaptive requirements imposed by this change in habitat are demonstrated by changes in the mechanics of the locomotory apparatus that makes climbing possible. Cursorial mammals have no clavicle and thus acquire great fore-and-aft mobility in the shoulder joint. The muscles for lateral movement of the arms and legs are reduced or modified to aid in running (*M. deltoideus, pars clavicularis* contributes to *M. brachiocephalicus*). Apart from the goat, hyraxes are the only mammals with no clavicle that climb trees. From their steppe-running ancestors, hyraxes have inherited three-toed feet which lack claws but which have rudimentary hooves. The radius and ulna are ancylosed and thus prevent pronation and supination. To make climbing possible in the absence of claws, the foot has acquired an adhesive sole with a large number of sweat-glands. To compensate for the impossibility of pronation and supination, the wrist joint is fixed in a position intermediate between the horizontal and vertical. When hyraxes walk on the ground or when they "walk" (on their sticky soles) up over rocks, the palms of their hands and feet are in a horizontal plantigrade position. When they climb up trees, they grab the sides of the tree trunk and move their palms into a vertical position. These movements occur by rotation about the wrist and especially about the inter-carpal joints. This inter-carpal movement is made possible by a novel serial arrangement of the carpals, a feature that was not present in their steppe-running ancestors.

Hyraxes inherited at least one character by which they were pre-adapted for climbing. All runners have facets in the wrist joint which prevent dorsal flexion of the hand. Such facets, which are retained by hyraxes, stabilize the hand during climbing and prevent it from tilting dorsally.

Fischer's project is not yet finished, but, from what has been outlined above, the importance of the various limitations is already obvious.

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GREEK CLASSICISM IN LIVING STRUCTURE?
SOME DEDUCTIVE PATHWAYS IN ANIMAL MORPHOLOGY

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ABSTRACT

Classical temples in ancient Greece show two deterministic illusionistic principles of architecture, which govern their functional design: geometric proportionalism and a set of illusion-strengthening rules in the proportionalism's "stochastic margin". Animal morphology, in its mechanistic-deductive revival, applies just one architectural principle, which is not always satisfactory. Whether a "Greek Classical" situation occurs in the architecture of living structure is to be investigated by extreme testing with deductive methods.

Three deductive methods for explanation of living structure in animal morphology are proposed: the parts, the compromise, and the transformation deduction. The methods are based upon the systems concept for an organism, the flow chart for a functionalistic picture, and the network chart for a structuralistic picture, whereas the "optimal design" serves as the architectural principle for living structure. These methods show clearly the high explanatory power of deductive methods in morphology, but they also make one open end most explicit: neutral issues do exist.

Full explanation of living structure asks for three entries: functional design within architectural and transformational constraints. The transformational constraint brings necessarily in a stochastic component: an at random variation being a sort of "free management space". This variation must be a variation from the deterministic principle of the optimal design, since any transformation requires space for plasticity in structure and action, and flexibility in role fulfilling. Nevertheless, finally the question comes up whether for animal structure a similar situation exists as in Greek Classical temples. This means that the at random variation, that is found when the optimal design is used to explain structure, comprises apart from a stochastic part also real deviations being yet another deterministic part. This deterministic part could be a set of rules that governs actualization in the "free management space".

1. GREEK TEMPLES

A Greek temple from the Classical period, such as the magnificent Doric Parthenon on the Akropolis (440 BC), served two main functions. The primary function is housing a divinity. This housing requires a small area, the cella, of the total space of the temple, because the cella accomodates only a statue of the divinity and provides space for a few priests. Thus there is an enormous discrepancy between the actually found huge building and the construction-model of the temple derived from the demands of its function. The discrepancy can be understood from a second function. The latter was to convince participants in the worship in front of the temple around an altar in the open air of the adequacy of the dwelling for the deity. Hence, a temple must emanate divine authority and harmony when it is viewed from the outside.

Greek architects of the Parthenon, like Ictinus and Callicrates, have apparently reached that goal of emanating divinity by designing huge colonnaded buildings around the small cella, according to the rules of a strict arithmetical or geometrical proportionalism. The available building technics and the applied materials, such as Penthelic marble and limestone in the Parthenon, created specific possibilities for and set also boundary conditions upon the design. This means that the structural design was an apparently functional formulation which was derived from the demands of the two functions, and which was carried out according to the architectural principle of proportionalism and the possibilities and boundary conditions provided by the applied materials and technics. Today the supposition of a functional design allows the explanation of the temple's construction. Therefore one constructs a theoretical model for the structure from the known functions, an architectural principle, building technics and materials, and compares it with reality.

A comparable deductive method is applied in animal morphology to explain living structure. There are, of course, some differences. Functions, materials and building technics are derived from living systems, whereas the derived theoretical model is compared to aspects of dead or living systems. Today this method is most successful because of the explanatory power of one architectural principle: "the optimal design". Optimal design in morphology and proportionalism in Greek Classicism are comparable as architectural principles. The easy acceptance of such principles usually rests upon a generally accepted believe or theory. The proportionalism arises from the believe that spatial regularity is harmonic and that harmony is divine. The optimal design is applied in technical sciences and it became for that reason a tool for morphologists who take the studied aspects of animal structure as machine-like. Moreover, Neodarwinian selection theory turned out to be transferable into optimization theory, and that meant for morphology the general acceptance of the optimal design as an architectural principle.

Close examination of the shape of the composing elements of the temples at the end of the last century has shown that small variations from the proportionality exist. They seemed random at first. But their sizes indicated that they could by no means be only the result of material and technical deficiences. Later, most of these variations turned out to be specific deviations, since their occurrence was correlated with particular positions in the temples design. Hence, the originally as stochastic, at random, interpreted variations from the deterministic proportionalism, turned out to consist of two parts. The first part is still stochastic and results from technical and material deficiences, but the second part is deterministic. The second part can be seen as a set of empirically founded improvements of emanation. This set has been found inductively by comparison of elements in many temples. The comparison resulted in, for example, a set of size-position correlations for the elements, which compose the shaft of a column. This set consists of a.o. the slight entasis (being an outward curve of the shaft of a column), the small upward tapering of the columns and their scanty inward leaning. These deviations were first interpreted as optical corrections to give the illusion of perfect straight horizontals and verticals [cf. 26]. Janson [13], however, argues contra this view. If these and other variations had served optical correction, they would certainly have been carried out invisibly. Furthermore, colonnades without the inward leaning certainly do not give the impression to topple outward. Therefore, Janson [13] concludes that these deviations must serve another purpose. They must be interpreted according to an illusionistic principle that differs from the proportionalistic principle. This second principle certainly improves the harmony and emanation of the proportionalistic principle.

A comparable feature is possibly found in animal morphology. Also here the architectural principle -that of the optimal design- is not always found satisfactory. If predicted values for structural parameters are tested and anomalies are found the following attitude is developed. Anomalies are automatically taken to be due to demands from yet unknown functions, to holistic, ontogenetic or historic constraints, or to boundary conditions from materials. But testing usually lacks. There is, however, never doubted the validity of the optimal design as the exclusive architectural principle. The reason is that this principle is taken axiomatically, so that it stays out of criticism.

It seems, however, fruitful to watch also for a second architectural principle as in the case of the Greek temple. This makes sense, because the optimal design excludes any neutralism or freedom, although the selection theory includes that aspect explicitly. Therefore, the question arises whether it is time for animal morphology to watch beyond the explanatory power of the optimal design.

The inductive method, being the search for related features by comparison, can answer this question as has been shown in the example of the Parthenon. Also deductive methods are able to give decisive answers. This paper proposes three such methods in order to test the optimal design. They will be exemplified qualitatively, they are intended to serve to set up rules for further quantitative analysis, and they indicate where a need for alternative architectural principles arises.

2. FUNCTIONALISTIC, STRUCTURALISTIC AND TRANSFORMATIONAL CHARTS

The time has past that the explanation in morphology is restricted to pure description [cf. 10,17,24,27] . Beyond descriptive and comparative morphology arose functional and ecological morphology with their interest in mechanisms and processes. It goes without saying that these two branches in morphology must also explain form or structure, otherwise they belong to different disciplines. Therefore structure descriptions must in any case occur at start and finish of all morphological projects. That means that feature selection as well as testing of predictions must include a careful description of structure. The interest in mechanisms in functional and ecological morphology evidently comes from the view that the animal's morphology is essential for its development and survival till progeny is assured. Hence, adequate functioning must determine the actual appearance of structure and not dead but living structures ought to be the subject of animal morphology. This development turns major parts of morphology into the biology of living structure.

Pure description of structure was the original method for the explanation in morphology. This method is, of course still valid. This method was succeeded by comparison of these descriptions. The method of comparison, the induction, is here the establishment of the co-occurrence of a series of form features with another series of form features. The comparison results in a next step in a general statement on the relation of different changes in these series. Comparison, however, is not only used between forms, but also between forms and another sort of features. This is found in the original functional and ecological morphology. Relating between form features and either specific physico-chemical/physiological internal features or ecological external features occurs in both mentioned areas, respectively. Whether such relations can be transferred into causal relationships is, of course, a matter of either physiology, ecology, evolutionary biology or morphogenesis, since they study processes not structures. Hypotheses, however, on causal relationships were often derived from the mentioned relations. Therefore, the results of comparative morphological research have substantially contributed to the development of theories on transformation, such as in the Darwinian selection theory of evolution, although too many comparative morphologists themselves failed to incorporate this theory [cf. 10,24] . Whereas the results from inductive research in functional and ecological morphology contributed much to the raise of the Neodarwinian and synthetic versions of the original selection theory.

Dullemeijer [8] , Alexander [1] and Gutmann and Bonik [11] showed that next to induction also deduction is necessary in functional and ecological morphology (cf. the hypothetico-deductive method according to Popper [20] applied for evolutionary biology in Dobzhansky [5]). For the use of the deductive method two recently common sorts of representation of a system have proven tó be essential: the flow chart and the network chart. The flow chart shows the flow of information, material and energy through a functioning system [cf. 4,30]. The flow chart represents a functionalistic picture of a system. The development of flow charts, however, should not be the final goal of any type of morphology. But the lack of proper models for the functioning or transformation of many systems forced functional and ecological morphologists to develop (parts of) the flow charts by themselves. This often confused the picture of these two areas of morphology, since many publications from these fields did not go beyond the development of such models, or they turned into exemplification of the Neodarwinian selection theory [cf. 9,32] .

The network chart for living systems can be looked upon in a similar way as in the sciences of architecture. The development of network charts should be the primary step in modern functional (pattern-)morphology [cf. 7,8] . Parts of such charts serve to formulate the architectural restrictions on the subdivision of the available space. Such restrictions could be set upon a subsystem that operates sub-optimal, so that the subsystem on itself could be maximized further than it actually appears. These restrictions arise from neighbouring systems or from the fact that a system must be a part of a whole. Such studies are becoming the particular subject of "Konstruktions-Morphologie" [23,28,29] and "Constructional morphology" [2] . The network charts should show a complete picture of all elements of a system and formulate the requirements for their proper role fulfilment in terms of spatio-positional needs. The network chart defines therefore the mutual competition or neutrality for space and position [cf. 6] of the elements in the totality of a living system. The network chart does not describe causal operation as the flow chart, but the three-dimensional organization. Thus it is a structuralistic picture.

Living systems always form a link in a chain of transformation. This feature forces a system into a process of internal selection that gradually narrows the channel of its possibilities for future changes. The exception comes about, of course, when epiphenomena occur which widen the channel again (cf. [36] , for an example on Actinopterygian lung development; and [41] , for examples on development of avian pharyngeal scrapers). Waddington [31] and Whyte [33] have formulated these concepts of canalization and internal selection, respectively, in an evolutionary context [cf. 8] . This suffices to make explicit that the subject of animal morphology must extend not only over dead and living, but also over transforming structures. Hence, functional design within architectural and transformational constraints must be incorporated for a full explanation of animal structure.

This paper proposes some deductive ways for explanation of structure and indicates that functionalistic, structuralistic and transformational pictures are clearly needed simultaneously. The starting point will be formed by functionalistic pictures like the flow chart. These methods have been worked out from the general scheme of deduction in morphology as has been suggested by Dullemeijer [8] . It is not the aim to give here a deductive method that starts from the network chart.

3. REPRESENTATION OF LIVING STRUCTURE

In the previous section I introduced the holistic approach in the specific version of a system's approach. The application of this approach, however, is preceded by acceptance of some axiomata. For a clear understanding of the use of the axiomata I will give pragmatic specifications of a few related concepts. They form together the basis for the proper use of the three deductive methods proposed in this paper. They will be given first (see Fig. 1).

Morphology studies living structure from the organismic up to the cellular level of organization. Therefore, it is most important to formulate the concept of "organism". It has become a common attitude to take the organism axiomatically as a pheno-genotype holon that is shaped by external environmental and internal physico-chemical factors and by a previous ontogeny and phylogeny.

The other axiom that specifies the previous one further, is to look upon the integrated totality of an organism as a system. That means that the organism is taken as a hierarchically organized integrated network of mutually connected elements. For the 'being a holon' in the first axioma and the 'mutually connected' in the further specification a unifying principle must be formulated. Role fulfilling is applied as the unifying principle, and that means on the organismic level operating in order to survive for procreation. This leads for the description of an organismic system to a tripartition of selectable sorts of characters. These sorts of characters are: structure, action and role. The choice of the system concept determines that the selection of parameters is guided by the question "how, by what and for what does a system fulfil a role?" Hence, the selection of structure and action parameters is primarily determined by that of the role of a system.

> Some of the just-mentioned terms need a brief specification. The concept *system* is understood as a group of living elements connected by their causal and mutual spatial relations, and the role they serve as a unit. The term *role* means here the service of a system in a supra-system. The concept role is taken equal to the biological role or biological function as it has been used in common practice at the organismic level as defined by Jeuken [14:41]. The next term, *structure*, is defined as any distinguishable extension in space, that can be measured in terms of distance, position, size and/or shape. Therefore, the term is taken as included in the concept of structure. This circumscription is similar to that by De Wilde [35:5] for form. The next concept, *action*, is taken to be any change in spatial arrangement on whatever level of organization, that can be measured directly

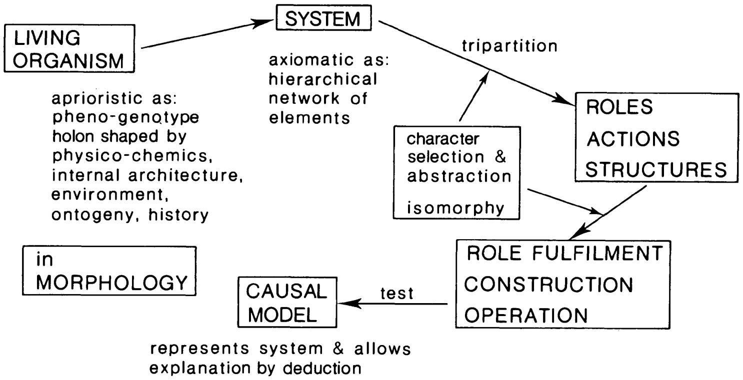

Figure 1. Subsequent axiomatic, selecting, abstracting and modelizing steps through which an animal feature runs prior to any deductive explanation of its living structure. A pheno-genotype holon is taken as a system that is described by way of a tripartition in its characters which are then connected in a flow chart. The causal model is (part of) a flow chart that in a purely functional design will be bounded by constraints from internal architecture (network chart), ontogeny and history (transformation charts).

as movement or indirectly as change of a physical parameter like electric activity. Finally, the term *element* finds a universal application in morphology [cf. 8] , which is comparable to that of the term taxon in systematics. An element is therefore any group of related structure parameters, with or without action or role characters.

The first step in the subject selection results in a rather crude qualitative abstraction of a system in structure, action and role parameters. The next step in the analysis selects from these three sets of parameters a relatively small number of data. These three sets are called the construction, operation and role fulfilment, respectively, as soon as they are clearly related in a model for the mechanism of the studied system. This model goes first through a qualitative phase, which should be followed by a quantitative phase. The model has been called a *causal model*, since it describes not only the spatio-temporal sequence of events, but also how the construction operates in order to fulfil a role. It goes without saying that each causal model must be tested.

A *model* is defined according to Rapoport [21] as a fictitious representation of the state of affairs under consideration that allows the application of deductive reasoning. The testing procedure must be such that the *isomorphy* between the original system and the causal model is accurately enough to allow the type of deduction proposed in the following sections.

The applied concept of organism needs now two further specifications.

The first is whether a system is looked upon as open or closed. All living systems are open. The proposed deductions are intended to include the use of mechanical and cybernetical laws. This requires to formulate the system (hence, organism and causal model too) as being closed. The next specification is on the existence of time order. Although mechanics is intended to be used, organismic systems are taken as having a one way time order.

Functional morphology apparently did not always reach further than the production of causal models for the mechanism of a system, as witnesses the sigh in so many ecomorphological studies like: 'we first must know more about the functional morphology of avian feeding ss.' [12,15,16,34]. But these causal models form on themselves only half of the story of explanation in functional morphology. Also physiology, ethology and ecology produce such causal models for mechanisms or processes on the organismic level. The difference with morphology, however, is that, where these research areas proceed to raise better and better causal models of the system by using morphological elements as stable invariable facts, morphology will use such a causal model as invariable in order to deduce and predict, yet unknown, structural characters. Hence, in morphology the mechanism or process is taken the stable feature. The meaning of producing causal models - apart from producing (cor-)relations by the inductive method - in functional and ecological morphology is that as soon as a system has been represented by such a model, explanation of structure by deduction becomes possible.

The traditional subjects of ecological and functional morphology are the mechanical systems on the organismic level which operate on the interface of the total organism and the environment, such as feeding, locomotory, protective, and respiratory plus circulatory systems. The neurosensorial systems should, of course, be incorporated also. A first common representation of the complexity of a system is the already mentioned flow chart of the composing subsystems that includes the informational feedbacks. The flow chart is in the present terminology a causal model or a series of causal models. Usually not the complete system is taken as the subject to study, but - for practical or traditional reasons - only one or two parts from the total flow chart are selected.

> For example, the flow chart for the feeding system of birds shows a series of some eight causal submodels. They connect changing muscle action with moving bones (1), these with moving connective tissue elements (2), these with moving epidermal elements (3), these with

moving food (4), this with changing proprioceptor, taste and touch signals (5), these with integrative brain action (6), these with alpha/gamma motoneuron action (7), and these with changing gland or muscle action (8) (see [37:428] for explanation). Examples from ornithology for qualitative causal models of step 4 are the slide-and-glue model for transport of seeds through the mouth of pigeons, and the suction-pressure-pump model for straining in mallards [39,40,42], whereas Kingsolver and Daniel [15] formulated a quantitative capillary model for nectar feeding in hummingbirds.

Such submodels selected from a complete flow chart are often taken as representations of the complete system. It is just this step of particular representation that allows deduction and prediction of yet unknown structural features.

Three sorts of explanation by deduction will be proposed: deduction of parts, in which specifications of yet unknown structural characters of apparently functioning subsystems are predicted; the deduction of compromise, in which balance in structural characters is traced; and the deduction of transformation, in which prediction of changes of structural characters is formulated.

4. DEDUCTION OF PARTS OF A SYSTEM

A first method for the deductive explanation is used for specific structural characters on a level of organization that is lower than that of the studied system. Now two possibilities for the sort of characters that can be deduced come up:

1) The first one deduces size, shapes topography, position, relative amount or quantity of subsystems, which either are supposed to be present or known to be present 'in some way'.

2) The second possibility is to deduce the construction of a system. This is done from demands derived from functioning/role fulfilling, from knowledge of presence of all sorts of subsystems, and from the application of the optimal design as the architectural principle. The first possibility will be worked out.

The procedure is as follows (Fig. 2). A system with one role is selected. Then follows a morphological analysis which must describe the system as extensively as possible, so that a most detailed description of the constructional and operational data is made possible. The role fulfilment is now carefully defined in terms of tolerance, performance and efficiency. Then the causal model is formulated and tested. This formulation is at first qualitative and should then be transferred into a quantitative one.

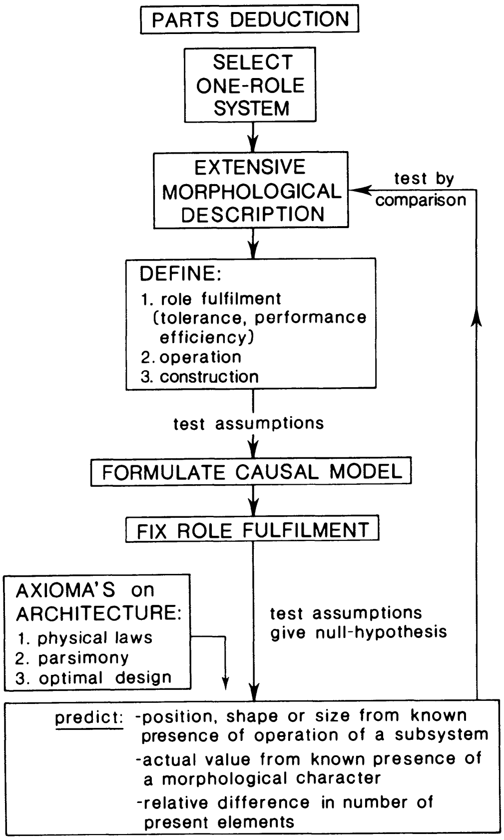

Figure 2. Subsequent steps in the procedure of the explanation of living structure by deduction of the parts. This method explains structural features of subsystems from their functioning in a wider system.

Now the role fulfilment is carefully defined, first qualitatively and later also quantitatively, if possible. From this stage in the analysis morphological characters can be deduced on a lower level of organization.

The deduction requires several specific suppositions. They restrict, as in any deduction, the general validity of the final conclusions. There are three such suppositions, which have a large axiomatic content. The first one is that physical laws hold under all circumstances in which the subject is studied. The second is that nature is taken to "solve a problem" always in the most simple way (the parsimony principle). This principle does not say anything on the costs, neither on the effects of the "solution". This is given by the third supposition, which says that the simplest solution is always realized according to an optimal design (the optimization principle).

> "*Optimal design*" carries two notions. The first notion is that of the minimum principle [cf. 9,22], which indicates that any construction has been built with the least possible amount of material, energy and time. The second notion holds that any role fulfilment is taken to be carried out by a construction that operates optimally efficient when it is in use. The operating construction is called the 'mechanism' of a system.

The previous set of suppositions is referred to as the axioma of "the architectural principle of the optimal design". Now the deduction can be done. The nulhypothesis should be tested. If additional assumptions must be made, they need to be tested too. Several possibilities for prediction of morphological characters arise. These are: 1) the position, shape or typography of a subsystem can be predicted from supposed or known presence of a particular subsystem; 2) the size of a morphological character can be predicted from its presence; 3) the difference in number of morphological elements in different comparable subsystems. The test of the predicted characters is the comparison with either the original or a renewed description of the actual structures. Since the prediction is derived from the role fulfilment, the predicted structural character is, if confirmed, explained functionally.

Structural constraints clearly play a role. This occurs in the procedure when there is competition for space between an element that is already part of the causal model and an element that is deduced from the causal model. The first element is then taken as independent (stable and invariable), the other as dependent (variable). The example below shows this when is stated: the mouth lacks space to carry a huge tongue in which enough mucus can be stored for fast seed transport.

High speed film analysis of pecking seeds by pigeons shows that seeds are transported through the mouth by a spectrum of possibilities. They range from the well-known catch-and-throw movements of head and beak, while the tongue does not move, via a series of intermediates to the slide-and-glue mechanism in which the head does not move at all and the tongue transports the seed. For the latter the seed must be glued to the tongue, which assumption has been confirmed from careful high-speed film-analysis. Hence, a sticky substance must be present on the lingual tip when it is pushed against the seed during lingual protraction along the mouth floor. Mucus is the only substance in living organisms known to be usable for this purpose, and glands are the only organs known to produce mucus, so glands must be available in the system. The simplest solution for the incorporation of glands is to put them in the tongue itself. However, this would interfere with two other more dominant characteristics of the tongue necessary for the food transport. These are the continuous flexibility and the smooth lingual surface. They would be disrupted so that the action of gluing a seed cannot be carried out; further, the tongue would become too big for any lingual movement if the huge volume of required mucus was stored in the tongue. The second simplest solution for the incorporation of glands is that the tongue scrapes the mucus from the mouth floor during protraction. This would require that the orifices lie along the stretch of protraction of the tongue. The orifices must face dorsorostrally. The glands must run longitudinally and the ducti efferentes must lie at their rostral ends, they must be elongated and large. If so, then these glands would be emptied by lingual protraction and the tongue would scrape off the mucus from the mouth floor. The glandulae mandibulares anteriores have indeed such a structure and topography [40:89].

A very clear example of this type of deduction of parts is given by Berkhoudt [3]. He deduced the position and the relative density of sensors for two types of touch qualities, which are known to be monitored by corpuscles of Herbst and of Grandry, in the mouth of the mallard. The deduction was based upon causal models for pecking and straining.

5. DEDUCTION OF COMPROMISE

A second pathway of the deductive method clarifies comrpomises in structure.

The procedure is as follows (Figs. 3 and 4). Select a structural feature that is involved in several roles; for example, the beak of Anseriform birds is used in straining, pecking, grazing, dabbling, biting and drinking. Select and define the systems which belong to these roles, describe their morphologies and formulate the respective causal models in a way as has been described in the previous section. Define then the role fulfilment in terms of tolerance, performance and efficiency for each of the causal

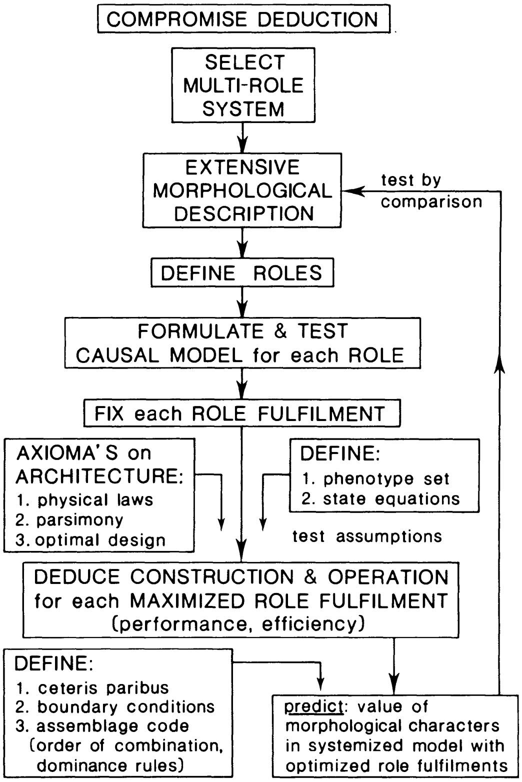

Figure 3. The procedure of the deduction of compromise. The operating construction is maximized theoretically for the different roles of a system. These maximized models are re-assembled into one model which for testing is compared with the original system.

models. The next step in this procedure is the theoretical maximization of the role fulfilment. To arrive at this goal one could ask the question: how could the causal model be improved if the other systems had been absent? This results in maximized causal models, which will be different for each role. The procedure for this theoretical generation of maximized models carries some limitations and rules. First, the before mentioned architectural principle of the optimal design governs the deduction, and second, there must be formulated which parameters are taken to be changeable and

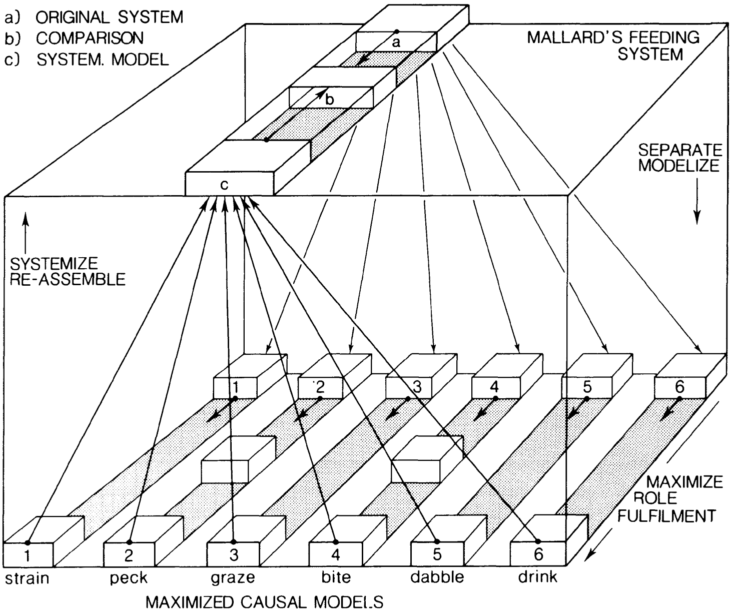

Figure 4. The method of the deduction of compromise exemplified for the feeding system of Anseriform birds. The system also plays a role in several other systems such as for preening, fighting, heat exchange, communication, etc. Whether these originate from epiphenomena or are due to deterministic influences should be investigated by stepwise addition of their maximized operating construction.

which not. In other words it must be formulated what is taken as the changeable "phenotype set" and what are the stable "state equations" as Maynard Smith [18] indicates this step for ecobehavioural models. For both sets the assumptions must be tested. Once the separate maximized causal models have been described the step to the prediction can be made by re-assembling these maximized models into one model. This step is called the systemization of maximized models, and results in the so-called systemized model in which the different role fulfilments occur in an optimized quantity. The deduced construction of the systemized model forms now the prediction for the actual structure of the system. This is tested by a comparison with the original or renewed description of the morphology.

The deduction of the systemized model has some restrictions, which originate from the structural surrounding. There are three types of restrictions, which should be read from a network chart. First the so-called ceteris paribus principle. This principle defines that in the studied subject only the selected systems are allowed to change and all other features stay constant. Hence, the selected systems must be taken to operate within invariable surrounding systems. (The example mentioned below shows this where bilaterality is introduced.) The second restriction is that the re-assemblage necessarily introduces choices about dominance, since (active) elements will be competitive for space, position, energy, material requirements, etc. if the available capacity becomes limiting. As a result of this necessity to make choices on dominance, as well as by the fact that only two maximized models can be systemized at once, an assemblage code is needed, which formulates the dominance rules and the order of combination of the maximized models. (The example mentioned below indicates this where respiration is given priority over feeding.)

This second pathway for deductive explanation is largely functionalistic and bounded by structuralistic restrictions. This will briefly be illustrated the qualitative deduction of the length of the pharynx of a pigeon.

The deduction of the length of the pharynx will be shown by following the subsequent arrows in Figure 5 from bottom to top. The avian pharynx has been defined as the area between the lingual wings and the ventral pharyngeal scrapers, which lie dorsocaudally from the larynx. The pharyngeal floor serves as an element in the systems of feeding, drinking, respiration, vocalization and heat exchange. The feeding, drinking and respiratory systems are selected as the dominant ones and the causal models are as follows, as far as they are relevant for the pharynx [cf. 38,39,40,42].

The fastest seed transport through the pharynx occurs in two steps. At the rictus level the seed is fixed, while the tongue is protracting so that the depressed lingual wings slide rostrad underneath the seed and the seed then rests upon the lingual base. Now follows the erection of the lingual wings while mucus is produced by glands in the base, so that the seed is kept adhered to the base during retraction. Now the total floor of the pharynx retracts and the seed is carried caudad and pressed against the caudal palate, where it sticks to this mucus area. The floor protracts again and the lingual base, the larynx and the depressed pharyngeal scrapers run rostrad underneath the seed. Prior to the next retraction the scrapers erect and they scrape the seeds off from the palate into the

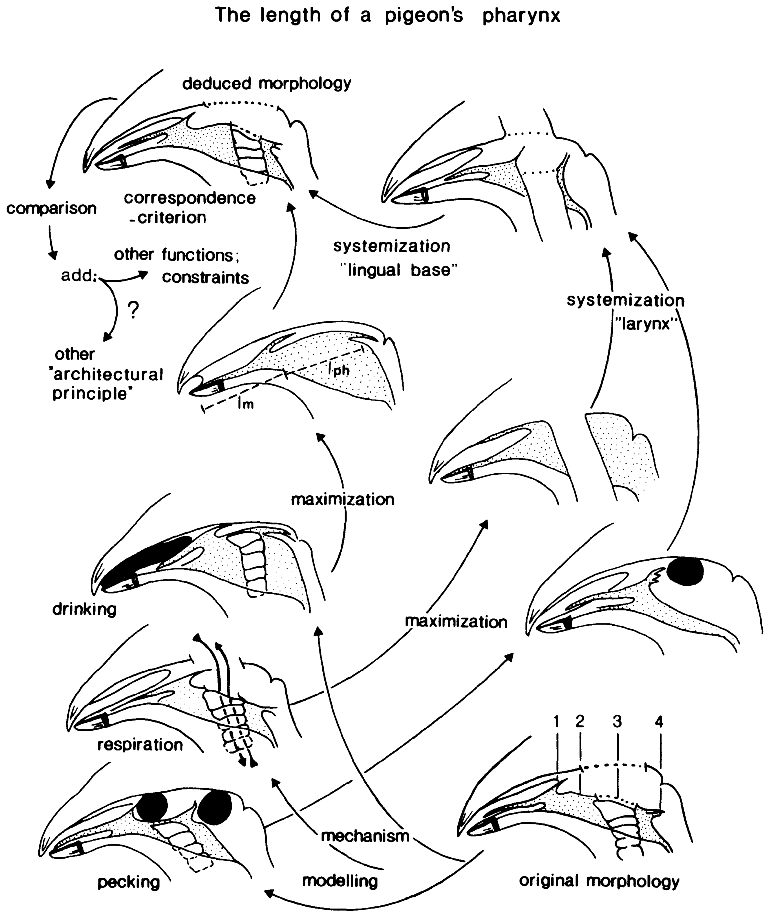

Figure 5. The length of a pigeon's pharynx explained by separate maximization of the pecking, drinking and respiratory system in the pharynx and subsequent systemization of these theoretical models. Pecking is maximized by coinciding the lingual wings with the pharyngeal scrapers, drinking by giving the wings and scrapers such a freedom for movement that a continuous flow of water can be generated, and respiration by connecting internal choana and larynx with a straight tube. Assemblage of maximized pecking and respiration introduced a valve construction, the larynx, whereas the assemblage of drinking adds a completely flexible area, the lingual base. 1. lingual wing; 2. lingual base; 3. larynx; 4. pharyngeal scraper.

esophagus. Hence, at least a two cycle movement of pro- and retraction is necessary to carry a seed through the pharynx from mouth to esophagus. From the elements in the floor of the pharynx only the larynx is involved in respiration. A 'drill-chuck' model has been described for the laryngeal mechanism. The analogy between drill-chuck and larynx is as follows. A drill-chuck comprises a set of graspers which is resiliently attached to the inner side of a constrictable ring, while the tips of the graspers point out of the ring. Ring and graspers are now compared to crico-procricoid ring of the larynx and the pair of arytenoids, respectively. The laryngeal ring and the graspers have elastic components, which keep the apparatus during rest in an intermediate open position. The larynx is actively kept open during respiration and it is closed by a reflex during food or water passage.

Drinking in the pigeon is a double suction mechanism. During each cycle of a series of pro- and retractions one swallow is carried from the beak tips to the esophagus. This occurs in two steps of suction. First the lingual retraction in a hardly opened beak causes suction of water into the mouth as a piston in a cylinder. Then the water comes to a rest prior to a jump over the pharynx floor. The momentum required for this jump originates from a sudden erection of the pharyngeal scrapers so that their tips are pressed against the palate, by which the pharyngeal floor must depress, so that a lower air pressure develops in the pharynx which forces the water from the mouth into a caudad move over the larynx.

The next step in the procedure is to maximize the role fulfilments in the pharynx. The pecking system is maximized by making the lingual wings coinciding with the pharyngeal scrapers, so that no pharyngeal floor exists, and hence no time is needed for the passage of food. The respiratory system is maximized by omitting the larynx and elongating the tracheal tube to the internal choanae. The drinking system is maximized if the full cycle transports water rather than only half of the cycle. This can be arranged by recombining the order of the actions of lingual wing and pharyngeal scraper as follows. The scraper is brought in a fully protracted and erected position when the erected lingual wings are at the end of their retraction. The next step is that the tongue should run rostrad with depressed wings, while the scrapers run caudad in erected position. Hence, the scrapers take over the suction of water into the pharynx. The reverse occurs when now again the wings erect and retract, while the scrapers protract in depressed position. Now the wings suck the water in and they push the preceding column of water in mouth and pharynx caudad. By this arrangement the water inflow becomes a continuous stream, while the larynx is omitted from the construction.

In the proposed procedure follows now the assemblage, the systemization. This requires an order of assemblage. It is supposed that air and food passage are dominant over water passage by suction, so that they are systemized first. Water can also pass with the food, so that food passage can be taken dominant over water passage. Respiration is in all vertebrates independent and relatively uninfluencable, so that this system is taken as the most dominant one.

The assemblage of the maximized air and food passage mechanisms must introduce either a sphincter muscle or a valve apparatus for two reasons. The applied ceteris paribus principle leads in this example to the acceptance of bilaterality and a median crossing of both tubes, since the systemized model must fit to surrounding elements. Further, the parsimony principle introduces the non-simultaneous use of both tubes, whereas the optimization principle introduces a fast steered gape of a rigid mouth at the entrance of the trachea and this consequently leads to a valve apparatus that separates the two. The dramatic drop in air transport capacity, even when the diameter of the trachea decreases slightly, limits the minimal size of the mouth of the apparatus. This leads to a median bivalvular apparatus with an inner transverse diameter that equals the diameter of the trachea. The larynx has the same general specifications. The assemblage of the drinking mechanism with the previous assembled model requires that the length of the pharynx floor should be equalized to the length of the mouth. This leads to the introduction of an area that is comparable to the lingual base, since the mouth is longer than the larynx. The final step in the procedure is the comparison of the predicted length with the actual one. Yet unpublished data show that the average length fits reasonably well, however, a wide variation is found.

Such a wide variation can mean that most individuals are anomalies. This feature does rise the question (within the framework of the proposed deductive method): Is the introduction of yet unknown functions and/or constraints able to cause a wide variation in the predicted length? Alexander [1] assumes a safety factor for the completion of a gap in the explanation of bone structure, being an over-strength. The concept has been borrowed from architectural sciences and it fits well as an axioma for living structure, since it roots so easily in the selection theory. The problem is that the size of this factor cannot be determined and it should be variable. Also Dullemeijer [8] faced the problem. He suggested to solve this by doing the deduction from the maximal load that ever occurs during a life-time. The safety factor can be assumed to have a variable value, the maximal load not. But even if a variable safety factor for "the length of the pigeon's" pharynx could be formulated in each of the three mechanisms, the question arises whether we must look for additional architectural principles. The question is what decides about actualizing of a certain factor in each specific case? Neither the first part of the optimal design (minimal energy and material for construction), nor the second part (use of the construction is optimally efficient) can fill this gap. Concluding, it can be stated that the actual structure and length of the pharynx floor can be seen as a cumulative compromise between the three different lengths and structures in the three maximized models. Further, a preliminary second conclusion can be added. Within certain boundaries the length and structure of the floor of the pharynx is either a neutral issue, or bounded to yet unknown rules for a second architectural principle that arises from transformation.

5. DEDUCTION OF TRANSFORMATION

A third pathway of the deductive method can be used for developmental models, hence for transformation. That means that the deductive method is made applicable for explanation of structure along the ontogenetical and historical time axes. This pathway can range from the relatively simple case of a one-type transformation (e.g. only size increase, or only increase of biting power) in a one-role system, to the highly complicated situation of a multi-type transformation in a multi-role system. Two examples will briefly be described: a one-type change in a one-role system, and a two-type change in a two-role system.

The procedure for the deductive method in the one-type change of a one-role system is similar to that of the causal model (see Fig. 6) for the deduction of the parts. The causal model is changed theoretically in a continuous series of models by applying a transformation function. The formulation of this series is, as has been shown in the previous sections, bound to the axiomata on the architecture (physical laws, parsimony

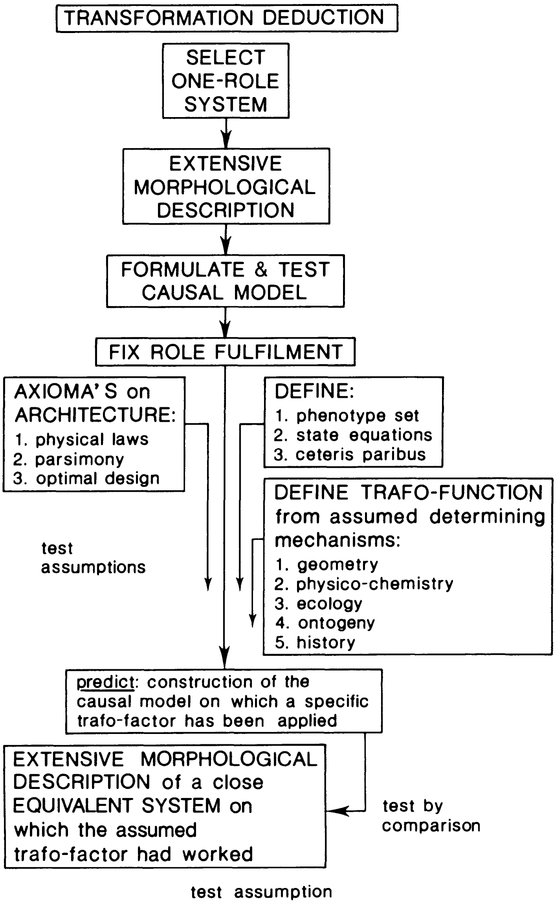

Figure 6. Subsequent steps in the procedure of explanation by the method of "transformation" deduction. Morphological features are taken to be explained, whereas the causal models and the transformation functions (wherever they originate from) are taken stable and invariable. The test of predicted characters is a test on reality value, thus whether they are realizable. Predictions must be compared with equivalent systems on which assumed or real transformation factors have worked effectively.

principle, optimal design) and further to the phenotype set, the state equations and the ceteris paribus principle. Then follows the choice and the subsequent definition of the applied transformation function. Transformation functions can originate from five different sources: 1, geometry;

2, physiology and/or physico-chemistry; 3, ecology; 4, ontogeny; 5, history.

Each of the sources mentioned for transformation functions needs a short comment. The geometrical transformation is a coordinate transformation applied to the construction of a causal model. Such a transformation leads to an explanation of structure that is based upon a mathematical idea. This is close to D'Arcy Thompson's coordinate transformations [cf. 25], but it is now applied to the parameters of a construction of a causal model, rather than to outer shape.

Physiological or physico-chemical transformations arise from bringing the causal model theoretically under changed internal conditions, so that, among others, other physiological or physical laws are going to play a role. For example, the internal conditions change drastically for supply of materials when the size of a small spherical organism is increased largely. It is then a must to add a circulatory system to that of diffusion, so that each element is properly provided with materials. Similar examples can be found for locomotion, information transfer, etc.

The ecological transformation arises from bringing a causal model theoretically under changed external conditions. This is clear from questioning: how should the causal model be changed if it had to fulfil its role maximally efficient under particularly changed external conditions. For example, change in hydrostatic pressure, in temperature, in density of competitors, in food composition; or more explicitly: change in density of the substrate in which a sandpiper probes.

The transformations of a causal model as a result of either internal physiological or external ecological changes are theoretical ones. They do not explain structure as resulting from any real order in ontogenetic or historic change. They, however, can do that under the following condition. Then a particular morphogenetical or evolutionary theory must be applied that describes the relation between the change of either in- or external conditions and the theoretical transformation of the causal model. In this way morphogenetic and evolutionary morphology arise from functional and ecological morphology.

At this point it is time to discriminate between two types of models which are well-known from ecology and which are relevant for the present deductive procedure too: the ultimate and the proximate model. The causal model is an ultimate model since it describes a situation, but it does not elucidate anything on 'how that situation came about'. The theories which deliver the transformation functions carry the proximate models which are used here to develop a theoretical series of ultimate models.

After the deduction of a series of causal models, a procedure is needed to test the reality value and thus the explanatory value of the predicted models. Therefore, first one specific value for the transformation is chosen and the causal model is changed according to this value; hence one stage from the total series is selected. Then a real, similar or equivalent system is selected, for example in a different species, which is close to the system from which the causal model and the transformation series have been derived. This close equivalent system is selected on the basis that it operates under the same condition as under which the theoretically changed causal model has been brought. The relevant morphology of this nearly equivalent system is now described and compared to the construction of the changed causal model.

The previous section shows the procedure for a one-type transformation. This has been exemplified in section 5 for a three-role system: the maximization of the pecking, drinking and respiratory systems in the pharynx of a pigeon. This example served compromise deduction, so that no test on reality value for maximization was included. This volume, however, comprises a beautiful example from Otten (this volume) that is close to the proposed procedure. Otten maximized a quantitative model of the kinematic part of the feeding apparatus of an almost biter-*Haplochromis*-species for biting force. The maximized model was compared with a biter-*Haplochromis*-species, in which all the predicted constructional shifts were found (the only exception was made plausible by a constructional constraint from the functioning eye). Thus the biter-fish was shown as the system in which the theoretical transformation function had worked.

A note should be added here about the difference between explanation in morphology and in evolutionary biology. The difference is not often made explicit and leads therefore to confusion. It is, of course, very attractive to find out whether the discussed transformations are also evolutionary transformations. Therefore, however, the forms and their historic order from almost-biter to extreme-biter must be taken as stable and invariable (independent) given features and the evolutionary process as the feature to be explained [cf. 9]. It must then be made plausible and be tested whether specific selection pressure really and effectively had occurred on the ancient almost-biter species, so that gradually developing biting-maximization is explained. This is evolutionary biology. It would have been evolutionary morphology if the evolutionary process was taken as the stable and invariable (independent) feature and the forms as the features to be explained. Specific quantitative knowledge about a certain effect of selection pressure on biting

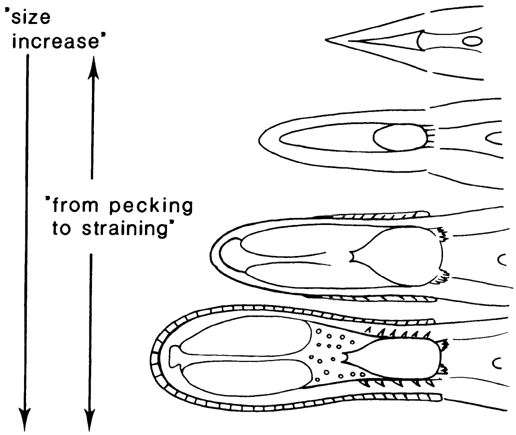

Figure 7. The change of the mallard's epidermal mouth structures during ontogeny explained by two transformations, one being allometric size increase, and second a specific change from a pecking "slide-and-glue" system into a straining "suction-pressure" system. The first is taken as a transformation function from ontogeny, whereas the second is seen as an ecological one in the sense that the system must be built as fitting best to the changing availability of adequate food.

force would give the transformation factor that must be applied to the original almost-biter causal model for a theoretical transformation. The outcome must then be tested against the real recent biter-fish.

Generally the studied systems are much more complicated, for example in a two-role system with a two-type change. This asks for the following procedure. The selection, the morphological description, the formulation and the test of the causal models for both roles have to be done as usual. Then the two transformation functions are selected and applied to the causal models. A simplified example will briefly be shown (cf. Fig. 7). As causal models have been selected the slide-and-glue model for pecking and the suction-pressure-pump model for straining (for this example also the catch-and-throw model for pecking is applicable; cf. [40,41,42]). As the first type for transformation an ecological one is assumed. It is supposed that external conditions change in such a way that a waterfowl's feeding system fits best by a gradual decrease of pecking performance and that simultaneously the need for a straining performance increases. To show this, both models must be maximized first and then systemized, reassembled, according a chosen mixture. The second transformation is an ontogenetic one, viz. a specific allometric size increase. The latter transformation is taken as superimposed upon the first one. This leads to the prediction that the constructions which are deduced in this series must be similar to the actual morphologies of a series of real systems on which the same transformations have really worked. For a test on the validity a real series is compared to the predicted series. This prediction has been visualized provisionally for the construction of the epidermal elements of the lower beak and tongue of Anseriform birds (Fig. 7). In mallards such a change from pecking into straining is found, as well as an allometric size increase [19]; however, further quantitative deduction and more substantial data are needed for proper testing.

The mentioned examples for deductive transformation in morphology start from the proposition that animal structure is able to transform without brake down of the total system. This means that change of a whole is possible only if the composing systems have a slight individual freedom for the realization of their construction, their operation and their role fulfilment. Therefore, a "free management space" must occur in living structure. The neutral issue, found in the previous chapter could be the place where such a free management space plays its role, if it is accepted that any transformation requires a certain amount of flexibility in role fulfilment and plasticity in construction and operation. Thus the apparently stochastic component that so far was implicit in the deterministic principle of the optimal design for living structure could nevertheless comprise another deterministic part, being an assumed set of rules that governs the actualization in the free management space. These rules should be traced empirically. That means that animal morphology must turn again to the method of induction if renewed evolutionary or morphogenetic theory is unable to find additional architectural principles.

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SOME METHODOLOGICAL REMARKS

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ABSTRACT

This contribution is an attempt to analyse the logic structure of the papers presented at the Lochmühle workshop in March 1984. The analysis is based on the definitions of the concepts of deduction and induction as can be found in textbooks on logic, and on the logic of argumentation and the structure of research programs as can be found in textbooks on philosophy of science.

Moreover, the analysis is evaluated against (1) the background of the investigator and through (2) the topics of discussion which were raised during the meeting. The deductive approach appears to be dominant with the participants although the presentation and the argumentation are influenced by the specific background, education and the profession of the investigator. The authors are aware of the limitations due to the use of these concepts in the above given definition used in this analysis. Therefore, one has to consider this contribution as an example of only one of the many possibilities to elucidate such a complex happening as an international scientific workshop.

1. INTRODUCTION

In every research program a specific procedure is followed, the methodology, which is affected by the philosophy, the education and background of the investigator. Consequently, a large diversity of opinions, aims and conclusions exist. Furthermore differences occur, although to a lesser degree, due to diversity in data selection, modeling, theory application, interpretation, prediction and testing.

The Lochmühle conference held in 1984 was aimed at analysing and comparing various approaches and procedures in animal morphology (see

Dullemeijer, this volume). At the beginning of the meeting we announced that we wanted to make, as an experiment, a reconstruction of the presented methodologies.

Nothing seems to give more satisfaction to a functional morphologist than an explanation of the most complicated construction by the most simple law or principle (see also the discussion by Zweers in this volume on the role of the principle of parsimony in the functional morphological methodology). The far-reaching consequences of simple mechanical and hydrodynamic laws for complicated phenomena like Moa legs (Alexander, this volume) and movements of cells (Bereiter Hahn, this volume), are just some of the presented examples of this common attitude. In the same way, we tried to elucidate the most complicated phenomenon present at the workshop - the structure of the functional morphological way of thinking of the participants - by means of the most basic laws of human reasoning: the classic logical rules of inference in relation to the special sociological aspects of the investigators, e.g. their position and background. For this purpose we designed a checklist containing a number of prescientific and scientific criteria. During the meeting and on the basis of the final papers in this volume we compared the methodologies with the aim to foster mutual understanding. Due to lack of time, caused by the vivid and inspiring discussions during the workshop, the presentation of our efforts had to be postponed to the present report in this special issue.

2. LOGIC MODES OF EXPLANATION

Most scientific statements can be described by the structure "Q because P", either presented in a conclusive manner, as the result of experimental research, or in a more hypothetical manner, as an address for an alternative approach. In logic two essentially different modes of this statement are distinguished. If we are interested in establishing the truth of Q, and P is offered as evidence for it then "Q because P" formulates an argument. If on the other hand, the truth of Q is regarded as unproblematic, as being at least as well established as the truth of P, but we are interested in explaining why Q is the case then "Q because P" is not an argument, but an explanation (Copie, 1971); an explanation, which presents a relation between P and Q. In the first case, if the argument P is a *sufficient* condition for the truth of Q, then the formal structure of inference of the first case is the so-called "Modus Ponens": "If P then Q. there is P, therefore Q" (= Q because P). It is one of the nine classic deductive modes of inference. When, however, the argument P is a *necessary* condition for the truth of Q (necessary in the logical sense that oxygen is a necessary, but not sufficient, condition for fire), then the formal mode of inference is false. This means that the argumentation is not by its structure apriori true. However, it does not rule out the possibility that it might very well be true in some special occasions.

Although the second case, the explanation, seems to be an argument at first sight, only a correlative relation between two or more phenomena is formulated. P nor Q will in general provide a real sufficient condition for each other. A more or less probabilistic relation is established and validated by means of inductive methods, like the five classic inductive "cannons" of Stuart Mill (1806-1873): The Method of Agreement, The Method of Difference, The Joint Method of Agreement and Difference, The Method of Residues, and The Method of Concomitant Variation.

For instance, when the shape Q is said to be caused by the theory or model P, the inference is called deductive only if the theory/model P provides without doubt the sufficient (and not only necessary) condition for the shape Q. In order to prove this strict constraint, a mathematical approach is chosen. If the theory/model provides only a necessary argument, or if both P and Q are considered unproblematic (evolution theory and diversity of shapes), then the way of argumentation is not purely deductive in its logical structure.

It has to be realized that these definitions of deduction and induction in logic, which were formulated more than two thousand years ago, have become subject to various interpretations, which exist due to various differences in the instrumental use of the concepts (in various branches of science). In its original shape the "modes ponens" houses two aspects which might obscure the discussions about deduction in science. One aspect is the "deductive structure of reasoning" and the other is the "deductive validation". In logic, deduction usually means a valid conclusion reached by the argumentation of the modes ponens. Recently, in philosophy of science "deductions" are described as rather specific research programs, which also lead to valid conclusions. The shift in accent is subtle, but crucial. The book "Concepts and Approaches in Animal Morphology" by Dullemeijer (1974) exemplifies in its title and content the shift towards deduction as a research program, as an approach.

Therefore, in this paper a distinction is made between validation and research program when deduction and induction are discussed.

research program	traditional	logic
deductive approach	Aristotelian deduction	deductive argument
inductive approach	inductive modes of Stuart Mill	inductive argument

3. REGARDING THE PRESENTED PAPERS

Among the 13 presented contributions three of the four aspects described above can be distinguished: deductive approach, deductive argument and inductive argument. Furthermore, these aspects seem to be linked with the context in which the explanation is given (cellular, organismic of phylogenetic) which shows a strong relation with the background and the institutional situation of the investigators. See table I.

4. INTERPRETATION OF THE PRESENTED PAPERS

The deductive argument, which urges the investigators to analyse sufficient conditions in the phenomena under consideration, is found among the functional morphologists Alexander, de Cock Buning, Dullemeijer, Osse and Otten. Firstly, this argument must rely on well defined relations (mechanical and kinematic laws: Alexander, Dullemeijer, Osse, Otten; radiation physics: de Cock Buning) having the logic structure "If P then Q", and secondly it has to rely on the testable prediction "P, therefore Q". See for instance Otten: If biting has to be optimalized, then these changes (1,2,3...7) in the construction of *Haplochromis elegans* have to be made. *Haplochromis nigricans* is a typical biting fish, therefore *H. nigricans* shows these 7 constructional changes in relation to *H. elegans*.

This deductive argument demands a mathematical formulation, or one of the same logical strength, in order to define the relations in a testable way, and a (living) object suitable for experiments. As a consequence, it is not surprising that these investigators design their actual research programs on the level of the organism and/or below this level (organ, cell, molecule). Without exception these investigators are connected to experimental departments of universities and their former education shows

TABLE I

X and x denote major and minor relevance

	name	institute	background	aspects to be explained	context				S2 ↑ S1	S=f(A)	induct/ deduct appraoch	math. model
					cell	org.	ecol.	evol.				
sub-group 1	Dullemeijer	Zool.Lab.	Funct. Morph.	shape ophidian ectopterygoid		X				X X X	D	X
	de Cock Buning	Zool.Lab.	Biophysics	relation shape & function ophidian IRorgan		X				X X X	I/ D	X
	Alexander	Applied Zool.	Ingineering	structure & function of Moa-leg		X				x X x	D	X
	Osse	Zool.Lab.	Funct. Morph.	function & construction protrusion in fish		X	X			X X X	D	X
	Otten	Zool.Lab.	Biophysics	shape cichlid fish jaws		X		x		x X x	D	X
sub-group 2	Zweers	Zool.Lab.	Funct. Morph.	form & function avian pharyngeal apparatuses		X	x	x		X x X	D	
	Reiff	Geol.Mus.	Paleontol.	shape & locomotion Hyraxes				X		X x	D	
	Bereiter Hahn	Inst. CellBiol.	Cell.Biol.	shape & movement of cells	X					X	I	
	Roth	Zool.Lab.	Neuro-Phys.	diversity tongue systems in salamanders		x		X	X		I	
sub-group 3	Grasshof	Zool.Mus.	Syst.	arthropod construction		x		X	X		D	
	Peters	Zool.Mus.	Syst.	tetrapod construction		x		X	X		D	
	Gutmann	Zool.Mus.	Syst.	change of general animal construction		X		X	X	x x	D	
sub-group 4	Bock	Zool.Lab.	Evol.Zool.	fitness and optimalization		theoretical treatise						
sub-group 5	An der Heiden	Theor. Biol.	mathematics	basic characteristics living organisms		theoretical treatise						

a strong affinity to physics.

The investigators of the second main group share their interest in phylogenetic questions. It is because of this evolutionary context, characterized by questions dealing with explanation of the transformation from one (extinct) structure into another (extinct) structure, that a deductive argument, in the strict logic sense, is not possible. The sufficient condition regarding shapes for instance, can never be proved, only argumented as being the most probable one. See for instance Grasshof (from analid towards arthropod), Peters (from fish towards tetrapod), Roth (primitive towards specialized tongue protruding mechanisms in salamander), Reiff (from digitigrade steppe runners towards plantigrade tree dwelling Hyraxes). Is their way of argumentation therefore inductive? The authors themselves emphasize their deductive approach! The apparent contradiction can, however, easily be solved if we distinguish the post-hoc presentation of the data and explanation in the paper from the research program actually followed by the investigator. The deductive research program with a deductive argumentation is characterized by the fact that it starts with a theory/model (mechanics, radiation physics) and its application to a special object unfolds, in its (calculated) consequences, relations which were not realized before. The same research structure can be found in the deductive research program with an inductive argumentation. When we start with the hydrodynamic principle or the principle of optimalisation and think thoroughly about the consequences of these principles for a special object (shape, cell, etc.) the deductive approach is followed. The difference with the deductive argument is that the deductive argument never provides new information. All data and relations are already given in the theory/model P. Therefore, the consequences can be drawn without doubt. Basic principles, without a (mathematical) reduction to a limited number of parameters, allow for collecting of more and more data, which support or deny these principles. The final proof will never be reached, and is doomed to stay probabilistic. Therefore, both research programs are deductive in their structure of approach, but the presented validation is of a different nature. The inductive validation describes the necessary conditions rather than the sufficient conditions (compare: oxygen is the necessary condition for fire). These explanations gain, in general, their value from the number of data affirming the proposed explanation. The obvious connections of these investigators with large data collections of (extinct) animals in musea provide the necessary prerequisites of the inductive argumentation of a deductive research program.

Regarding this simple classification, an exceptional position is taken by Bereiter Hahn and Roth. Both show an interesting contradiction of their background and the presentation of their research programs, between their prescientific and scientific conditions. Their background is without doubt an experimental one (respectively cellular biology and sensory physiology) and their approach is, we would expect, a (mathematical) deductive one. Their approach is, however, rather inductive: Bereiter Hahn gives a correlative description/explanation from a spherical celstructure towards a cell with a pseudopodium. Roth focusses on the necessary (not sufficient) succession of tongue structures in phylogeny. We have the impression that this remarkable situation is induced by the connections with respectively Gutmann and Wake, both thinkers in the field of transformation of structures in evolution.

Some last words should be spent on the five theoretical contributions. Bock proposed to approach phylogenetic problems from two sides. First, he proposed to extend the functional morphological research programs towards "fitness" of the organism, instead of the "optimal" performed activity. Secondly, he suggested to try to find some hierarchical interpendence of the essential constructional elements: bones, muscles, bloodvessels, nerves and sense organs.

Zweers analysed in detail the subsequent methodological steps which are used in his extensive research program concerning the functional morphological aspects in the facial-cranial area of ducks and pigeons. The presented examples of research show the deductive approach. The actual presentation and validation are, however, not of the nature of the mathematical deductive argument.

Reiff sketched the ideas of Weber and Seilacher of the role of morphology in the context of evolutionary biology. He suggested to investigate whether absolute constraints limit the range of possible organic forms at the three levels: a) historical/phylogenetic constraints; b)functional/adaptive constraints; c) constructional/morphogenetic contraints. We would like to remark that Reiff's interpretation of Seilacher "Konstruktions Morphologie" is equivalent to the Dutch interpretation of "Functional Morphology" (de Cock Buning, Dullemeijer, Osse and Otten).

The contribution of An der Heiden focussed on the concepts of "self-generation" and "self-maintenance" as main characters of all living organisms; concepts which express a fundamentally different point of view regarding transformation of structures. A similarly different position is taken by Gutmann. His question is not which optimalisational/adaptational steps an organism performs in successive transformations (filling a sub-optimal situation with an adequate adaptation), but by which adaptations an organism is able to remove an unfavourable construction. From this point of view the strategy of nature is exactly opposite in direction. The driving force is not an abundant production of pre-adaptive creatures of which some may survive, but on the contrary, we are dealing with a highly conservative system placing emphasis on energy conservation and expelling all energy consuming adaptations. The energy conserving and converting system was illustrated by the hydraulic principle in cells and organisms.

These theoretical contributions challenged the audience to reconsider the implicitly accepted contents of concepts and boundary conditions generally used in functional morphological research, and to look upon an object from different positions: fitness instead of optimalization, the ultimate absolute constraints instead of the proximate individual constraints, self maintenance and hydraulic principle instead of kinematic laws. Because these reflections belong to a discussion prior to the research programs and validations the shifted positions require a related unconventional set of selected data, a different orientation to systemization, etc. In other words, different completion of most of the subsequent steps described by Zweers (this volume) in the generalized research program.

In the next chapter some examples of the confusion are given, which arises when the participants (implicitly) enter the discussion from different positions.

5. DISCUSSIONS DURING THE CONFERENCE

The main purpose of this workshop was the critical reflexion on methodologies applied in the field of Functional Morphology. The discussion during the conference, in which the different approaches were confronted with each other shows again, although indirectly, the confrontation of the described methodologies/approaches (see Table I).

A number of times during the sessions, some differences in opinion became evident. We would like to summarize these differences, together with some methodological remarks.

1. As a reaction to An der Heiden's paper, Bock had some problems with the definition of viruses as selfmaintaining machines. This was the reaction of an ecologically thinking functional morphologist (Bock), to the attempts of a theoreticist (An der Heiden) to get some order in the chaos of living nature, by coining some definitions. Clearly the gap between the positions was to big to come to an agreement.

2. In a discussion between Bock, Otten and Roth as a reaction to Roth's paper, the mechanics and elastic components of tongue flipping were discussed. Here, the same language was spoken (that of mechanics) and the same practical problem solving attitude was adopted, resulting in a progression in ideas.

3. As a reaction to Roth's paper, Gutmann indicated that polarity of evolution is given by the process, and not from a series of character states. Roth agreed immediately.

4. Bock, Roth, Reiff and Maier joined a discussion in which Bock stated that selection force on each species is different, which was supported by Reiff. Roth replied that the way food is gathered can be done in several ways without differences in selective advantage (neutralist radiation), while Maier claimed that Roth showed selectionism anyway. It is very likely here, that the definition of the concept "advantage" is used in a different way: on the one hand, there is no obvious advantage between the different *mechanisms* of the tongue flipping, all specializations survived successfully (Roth), on the other hand, there is a clear advantage for each specialization of food-uptake, because they survived successfully as different mechanisms (Maier). This discussion could have been fruitful if there would have been more time, because all participants used the same language, that of evolution.

5. Osse, Alexander and Otten discussed protrusion mechanisms, as a reaction to the paper of Osse. They all used the language of mechanics, but lacked sufficient information to decide whether protrusion mechanisms show mechanical redundancy or can display several solutions.

6. Reiff, Bock and Gutmann discussed historical constraints in animal design. Immediately the discussion resulted in the division of taxonomic reasoning and functional morphology. Unfortunately, no cladists were in the group. Reiff temporarily defended this approach in taxonomy, although

he added that cladists often produce caricatures of adaptionists. The general acceptance of this position among the audience demonstrated the shared interest of the participants in functional aspects in contrast to form-features.

7. As a reaction to Alexander's paper on the leg of the Moa and its internal stresses, Bock stated that rare conditions of high stresses may have selective advantage, which Alexander took as information for the moment.

8. Alexander suggested a quantitative approach to Gutmann concerning energy conversion in organisms. This was a suggestion for further research but Gutmann replied with a defence. It is very likely that Alexander (and later Zweers and Dullemeijer too) intended to stimulate a quantitative approach rather than criticise positions.

9. Grasshoff, de Cock Buning, Roth, Bock and Gutmann joined a discussion concerning adaptations. Grasshoff and Gutmann stated that adaptations consist of escaping unfavourable situations (in the sense that the bony construction of the limbs diminished the unfavourable situation for terrestial locomotion by a fish-shaped ancestor). Roth feels that when more solutions are available, there are more possibilities to survive. Bock puts forward that there are multiple pathways of adaptation and not just one answer. Gutmann agrees with the bifurcation points of Roth: there are moments in evolution when two solutions are available. De Cock Buning suggested to divide conditions for adaptation into necessary and sufficient ones, with which Grasshoff agreed. This was a central discussion in which a common language was shared and it may well have been the basis for progression of ideas.

10. Reiff indicated to the functional morphologists in the group, that there exists a methodological problem when one only deals with functional morphology. From that point of view, it is always possible to look better and to explain differences in animal design in a functional way, without having to look at the evolutionary process. There was a general consent to this position.

From this summary, three aspects become apparent.

Firstly, most discussions are between members of different subgroups (see Table I for the division in subgroups). Only one discussion (number 5) was among members of the same subgroup and was actually a technical discussion. This was a discussion concerning further technical consequences without considering the presuppositions regarding the model and the methodology.

Secondly, most discussions were held using a common language, and whould therefore be indicated as useful or potentially useful. Only one discussion (number 1) showed a clear division in position, philosophy and language. Consequently, the discussion met severe problems regarding the definitions of concepts.

Thirdly, two discussions (number 4 and 7) did not lead to an agreement, although the same language was shared. In the case of the rare occurrences of stresses in Moa leg (number 7), clearly (evolutionary) information was missing to come to an agreement. In the case of the discussion concerning adaptation and selection of food-uptake apparatuses (number 4), a truly crucial but difficult point was raised, which could certainly have led to the development of new ideas. However, we did note that sometimes identical words (advantage, relations, successful) were used in quite different contexts (neutralistic, selectionistic) and (thus) with very different meaning. Before progression in the discussion on different ideas about evolutionary processes and functional morphological research programs can be made, one should clarify these concepts first in a meta-discussion. One solution could be to distinguish different positions within the shared language.

6. CONCLUSIONS

The above presented analysis does not intend to draw any normative conclusions regarding the different approaches among the participants. Some basic principles of reasoning, which can be found in every textbook on logic allowed an analysis in order to clarify the different positions within functional morphology as presented in the papers and related discussions during the Lochmühle meeting.

The analysis shows a shared fundament, which obviously binds the participants consisting of a) a strong emphasis on the functional aspects regarding the explanation of shape, size and positioning, b) the aim to relate evolutionary questions to functional morphological approaches, and c) a strong emphasis on the deductive approach.

Most of the differences which exist among these investigators can be either traced back to the specific background, education and type of institute of the investigator, or the presentation and validation of the deductive research programs.

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p. 259: Fig. 1. Disregard the angles α and β, consider only $\emptyset\alpha$ and $\emptyset\beta$. In the explanation substitute tgα by tg$\emptyset\alpha$ and tgβ by tg$\emptyset\beta$.
p. 264: In the 5th line from below the last word "not" should be deleted.
p. 266: In the 1st line, if the measure should read: in the measure.